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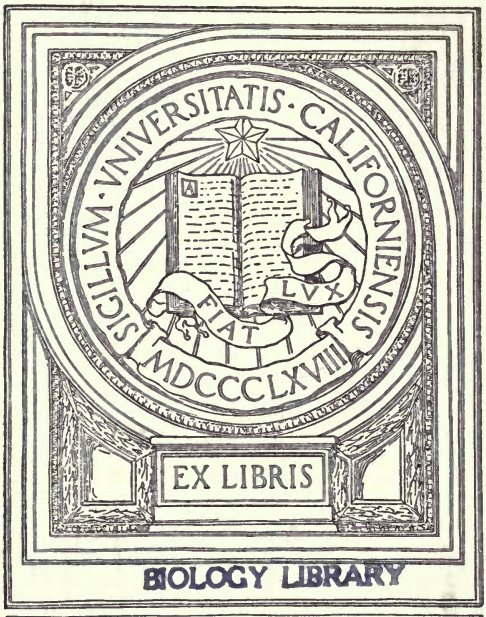

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ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. VI January, 1920 No. 1

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PUBLISHED UNDER THE
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THE NASAL ORGAN IN AMPHIBIA

WITH TEN PLATES

BY

GEORGE MARSH HIGGINS

Contributions from the
Zoological Laboratory of the University of Illinois
under the direction of Henry B. Ward No. 171

THESIS

SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS

1919

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INTRODUCTION

There is considerable literature upon the development of the chondrocranium of the Amphibia, but only a little of it gives adequate details of the process of chondrification of the nasal capsule in this class of vertebrates.

Parker, in a long series of extensively illustrated papers, (1871, 1876, 1877, 1881) was the first to give any adequate account of the development of the skull in the Amphibia; but his remarks, so far as the nasal capsules are concerned, are general and no detailed description of the parts or processes of chondrification are given. Born (1877) gives, in considerable detail, the process of chondrification in *Triton cristatus;* while Stöhr (1879) who also described the chondrocranium of Triton, paid but slight attention to the ethmoidal region.

Gaupp (1893) in his well known work on the cranium of *Rana fusca* discusses four stages in the development of the skull of the frog, treating all parts with more detail than any other writer. According to Miss Platt (1897) the nasal capsule in Necturus, to a great extent, chondrifies independently of the trabeculae; but she gives but slight account of the development of the fenestrated roof of the capsules. Winslow (1898) dealt with the chondrocranium of several of the Ichthyopsida, but his account of the development of the nasal capsules has but slight detail. Peter (1898) is the only one who has described the skull of any Gymnophione; while Terry (1906), who followed the history of the nasal capsule of Amblystoma through five stages, states that the process of chondrification in Amblystoma agrees closely with that of Triton.

The work covered by this paper was undertaken with the idea of ascertaining what homologies, if any, could be drawn between the nasal capsules of the various groups of Amphibia; and to determine in how far these structures would substantiate or alter the different classifications proposed for this vertebrate group.

The work was done in the Zoological laboratory of the University of Illinois, almost entirely upon the departmental collection. It was carried on under the supervision of Professor J. S. Kingsley to whom the writer wishes to acknowledge his sincere appreciation for the many helpful suggestions and his kindly attitude during the investigation and the preparation of this paper. I wish to acknowledge my best thanks to Professor A. C. Eyclesheimer of the University of Illinois College of Medicine, for the loan of several of his series of slides of Necturus.

THE NASAL CAPSULES OF THE URODELA

AMBLYSTOMA PUNCTATUM

Amblystoma was selected as the basis of these studies upon the nasal organ of Amphibia, primarily because of the larger number of stages available, as well as on account of its intermediate position among the Urodeles. I have studied and modelled seven stages of Amblystoma, which show the successive steps, progressive and retrogressive, in the chondrification of the nasal capsule of this Urodele.

A larva 11 mm. long (Fig.1) shows but few features of a nasal capsule. The trabeculae (*t*) extend forward along the ventral margin of the forebrain and in the region of the eye, each has developed a small dorsal crest, so that in cross section it appears triangular. At this stage the trabeculae do not unite, but each expands distally into a small rhomboidal plate, the cornu trabeculae (*ct*), which supports the anterior end of the nasal organ. In a slightly older stage, a few cartilage cells appear above the medial margin of the cornu trabeculae of the left side only (Fig. 41). These cells are the beginning of a bar of cartilage, which develops along the medial dorsal margin of the nasal sac, and is known in the literature as the ethmoidal column, a term used throughout this discussion.

In a larva 20 mm. long (Fig. 2), chondrification is much more advanced. Slightly anterior to the internal nares, medial trabecular processes have united in the middle line to form a broad planum basale (*pb*), which supports the anterior end of the telencephalon. This plate is broadly concave dorsally, its lateral margins being elevated, the result of the trabecular crests. Its posterior margin is straight and at right angles to the axis of the skull, but it meets the medial margin of the trabecula in an oblique angle, because of the converging lines of the latter. The anterior margin of the planum basale passes into the expanded cornua trabeculorum, which lie in practically the same plane as do the trabeculae. The cornua extend laterally and each is concave upon its dorsal surface (Fig. 42) and supports the anterior part of the nasal organ and the organ of Jacobson; while posteriorly it reaches about the level of the middle of the planum basale where its posterior lateral angle terminates in a short caudal process. The anterolateral margin of each cornu is at about an angle of forty-five degrees to the median axis of the skull.

Dorsal and parallel to each trabecula and the median margin of the cornu of either side is an elongate rod of cartilage, the further development

of the cartilage cells above the cornu trabeculae in the earlier stage. This columna ethmoidalis (*ce*) extends posteriorly to the level of the choana, lying medial to the olfactory organ and separating it from the forebrain. As yet it is distinct from all other cartilage structures, although Terry (1906) in a similar stage has described a connection of this bar with the crista trabeculae.

In this stage is the first appearance of a cartilage roof over the nasal organ. From the posterior tip of each columna ethmoidalis, a small plate has chondrified laterally which partially covers the olfactory sac above the choana. This is the beginning of the planum tectale, which in the later stages completely covers the posterior parts of the nasal organ. In this connection it is of especial interest to note that although the columna ethmoidalis chondrifies from in front backward, the planum tectale arises at the caudal limit of the column and develops anteriorly.

In the next stage (Fig. 3), several features have been added to the capsule. The crista trabeculae (*cr t*) is well developed and has united to the posterior end of the columna ethmoidalis (*ce*), thus forming a wide trough or cavum cranii, which supports the anterior end of the telencephalon. In front of the crista, each trabecula inclines slightly toward the median line to pass into the planum basale (*pb*), which shows but slight modifications from the earlier stage.

As yet the dorsal and ventral parts of the capsule are almost entirely distinct from each other, the only connection being by the crests at the posterior end (Fig. 4). On the other hand, the columnae of the two sides are connected by a narrow ethmoidal bridge (*pe*), which lies directly above the anterior margin of the planum basale and is formed by medial processes from each ethmoidal column (Figs. 4, 44).

Between this bridge and the basal plate are procartilage cells, which in a later stage are to form, with the pons ethmoidalis, a transverse wall of cartilage (to be described later) bounding the cavum cranii in front. Up to this stage there is no complete separation between the cavum cranii and internasal space, a condition which is permanent in Urodeles like Triton.

Each columna ethmoidalis is now wider than before, except at its extreme posterior end where it joins the crista. In front of the pons ethmoidalis, each column bends obliquely outward and forward from the axis of the skull and ends at the level of the tip of the cornu. A little in front of the cristal connection of trabecula and column, each column bears a lateral process which curves down over the choana. This is the beginning of the planum tectale (*pt*) forming the posterior part of the more complete roof of the capsule in the later stage. In the literature upon the amphibian nasal capsule, this tectal plate has been called the lamina cribosa; but from its relation to the olfactory nerve it is evident that it is totally different from the cribiform plate of mammalian anatomy, hence the proposal of the name used here.

Another cartilage arises from the lateral side of each trabecula, behind the choana, and the anterior margin of the cristal connection of the trabeccula and column. This has been called by the German writers, the palatine process; but it has no relation to the palate or the palatine bone, and is better called by another name, frequently used for it, the processus antorbitalis (*pa*). It extends laterally about as far as the cornu, and is destined to form a part of the posterior wall of the nasal capsule.

As yet there are no distinct olfactory foramina, but the olfactory nerve leaves the forebrain at right angles to its median axis and passes into the capsule through the large gap between the trabecula and the column, just anterior to the crista trabeculae.

In a 34 mm. larva (Figs. 5, 6)the process of chondrification which formed the pons ethmoidalis of the 25 mm. stage, has continued ventrally and posteriorly, so that the bridge has joined the planum basale and has extended back to about the level of the planum tectale of the previous stage. The result of this is the formation of a large median wall to the cavum cranii, the only openings left being the olfactory foramina which pass into the capsules at the lateral margins of this wall. From conditions which occur in other Urodeles this median mass is best called the planum verticale, although it is much thicker than in Amphiuma and the Caecilians. As will be seen in the sequel, this planum verticale may be defined as the cartilage connecting the nasal capsules of the two sides, beginning as a median dorsal pons ethmoidalis from the two columnae and then extending down to join the planum basale. The anterior margin of the planum verticale (*pv*) is deeply excavate, and together with the medial walls of the nasal capsule, it bounds the V-shaped internasal space in which the intermaxillary glands lie. The lateral margins of the verticale slightly extend over the medial margins of the nasal organs from the olfactory foramen to the tip of the capsule, thus forming the anterior part of the planum tectale, which is pierced by a small opening (*fni*) through which the ramus nasalis internus of the fifth nerve passes into the internasal space. Thus the planum verticale is a compound structure formed from the ethmoidal bridge and the columnae ethmoidales, uniting ventrally with the planum basale.

The posterior parts of the planum tectale (*pt*), which began in the last stage (25 mm.), now forms a broad curved plate which covers the caudal half of the nasal organ, and extends forward from the crista trabeculae to the level of the anterior margin of the foramen olfactorius. Laterally it extends nearly to the level of the gap between the caudal extension of the cornu and the antorbital process; the posterior margin of the tectale is oblique, its antero-lateral margin is slightly arcuate, while in front it is produced into a small conical process (Figs. 5, 6).

The expanded cornua trabeculorum (*ct*) do not differ greatly from those of the preceding stage. The lateral margin of each cornu is slightly arcuate

and the posterior lateral angle nearly meets the lateral margin of the tectale (Fig. 5). Medially and behind, the cornu is continuous with the planum basale, which has now extended laterally so as to form a partial floor beneath the medial side of the olfactory sac. In all Urodeles the produced postero-lateral angle of the cornu supports the organ of Jacobson (vomeronasalis). This relation and also that of the organ to the lateral part of the tectale is of great aid in determining the homologies of the more complex capsule of the adult.

The antorbital process (*pa*) is now larger, forming a plate rather than a bar, and its antero-lateral angle is directed forward as a blunt process which nearly meets the posterior process of the cornu and also the lateral margin of the tectale.

In the nasal capsule of a 45 mm. larva, only a few modifications need description. The capsule (Figs. 7, 8) has not increased in length, although there has been an appreciable increase in width and depth. With the greater development of the olfactory lobes there has been a corresponding increase in the size of the cavum cranii (*cc*). The olfactory lobes extend forward only as far as the caudal third of the nasal sac, so that the olfactory foramina look obliquely forward from the antero-lateral angles of the brain case. There is a gradual change during growth in the relative positions of the nasal sac and the forebrain. In the earlier larva, brain and olfactory organs overlap for about half the length of the nasal sac, while in the adult the sensory structures are almost entirely in advance of the tip of the olfactory lobes, approximating the anuran condition.

The planum verticale (*pv*) of this stage is shorter than before but its height is almost twice that of the 34 mm. larva; so that this stage marks the beginning of the reduction of the verticale which is so much smaller in the last stage to be described.

The only other features to note in this stage are the broadening of the tectale, which process has brought the foramen for a branch of the nasalis internus on to the dorsal surface of the capsule and the extension of the antero-lateral angle of the tectale, so that it now fuses with the postero-lateral angle of the cornu, forming the first appearance of a lateral wall to the capsule. The naso-lacrimal duct passes over this connection between cornu and tectale, and empties into the olfactory sac just above the anterior end of Jacobson's organ.

Procartilage cells are abundantly distributed over the anterior end of each olfactory sac, the anterior naris being terminal in all larval stages. From these cells, the anterior cupola is formed; a process which involves the shifting of the naris to its lateral position.

In a larva near the end of metamorphosis (Fig. 9) many changes of the capsule of the early stage have occurred. The general proportions of the capsule remain unchanged, although there has been a further reduction in

the length of the planum verticale, so that one-half of the entire capsule lies anterior to this median vertical plate. The width of the verticale is also reduced by one-half to accommodate the lateral development of the olfactory organs which now lie much closer together. The anterior surface is widely concave, its dorsal margin overhanging the ventral, thus forming a partial roof over the intermaxillary glands.

The planum tectale (*pt*) now covers the entire dorsal aspect of the nasal sac and extends from the region of the choana to the tip of the capsule where it has united to the anterior margin of the cornu trabeculae, forming the cupola (Fig. 9). This area is pierced by five small foramina. Four of these are in an oblique quadrilateral, the fifth, much larger, lying behind the others. Of the four, the anterior three foramina are for the branches of the nasalis internus which are distributed to the dorsal part of the snout; while the lateral foramen passes a branch of the profundus from the capsule. The larger posterior gap contains no nervous structures and apparently is the beginning of the resorption of the cartilage roof of the capsule. The medial surface of each capsule is marked distally by a small prenasal process (*pnp*) at the base of which is the foramen nasalis internus (*fni*), above described. On the dorsal surface of the capsule is a sixth small foramen for a branch of the profundus of the fifth nerve, the result as before, of the extension of the cartilage around the nerve.

The antorbital process (*pa*) has now united to the lateral posterior margin of the tectale, a condition foreshadowed by the close association of these parts in the earlier stages, thus inclosing a large foramen between the posterior margin of the tectale and the basal part of the antorbital. This is the foramen orbito-nasalis (*fon*) into which the caudal part of the nasal sac extends, and through which the nasalis internus of the fifth nerve enters the capsule. Lateral to this foramen, the united elements of the antorbital and tectale are directed obliquely forward, covering the lateral aspect of the olfactory organ. A branch of the profundus nerve and a blood vessel pierce this plate by two foramina just posterior to its connection with the caudal extension of the cornu trabeculae (Fig. 9).

As in the earlier stages, the organ of Jacobson rests upon the caudal extension of the cornu which extends more posteriorly, and has partially united to the fused tectale and antorbital. This union of the cornu to the posterior tectale has resulted in the formation of a new foramen, the infra-conchalis of Gaupp (*fen i c*), through which the anterior part of the organ of Jacobson extends to the laterally enveloping tissue (Fig. 46, *jo*). Thus this organ rests upon a shelf formed by the cornu trabeculae, while its anterior end extends through the foramen. This infra-conchalis is separated from the large lateral narial opening by the bar, which in the 45 mm larva connects the cornu trabeculae and the tectale. A deep groove occur- in the lateral wall of the planum tectale which leads to the posterior bound-

ary of the external naris, along which the naso-lacrimal duct passes to the olfactory organ (Fig. 45 *ld*).

This stage represents the highest development of the cartilaginous capsule in Amblystoma. The nasal organs are completely encased in cartilage, except for the external and internal narial openings. In the later stages studied, and in the early adult capsule, conspicuous gaps have formed through the process of resorption, giving way to the various membrane bones that enclose these sensory structures in the adult. That the completeness in the development of the capsule, which has been attained in this stage, is in some way associated with metamorphosis, is very evident, and it probably represents the end of the larval period.

The cartilaginous capsule of the adult Amblystoma (Fig. 10) results by reduction and specialization of structures present in the stage just described. Increase in the size of the sensory structures necessitates a capsule of enlarged dimensions, although the proportions are relatively the same. The planum verticale is reduced to a narrow bar which is relatively more posterior in respect to other capsular parts; its anterior ventral surface is deeply excavate, the dorsal surface covering the intermaxillary gland to a greater extent than before.

Strikingly characteristic of the adult cartilaginous capsule is the large five-sided gap in the roof which completely exposes the dorsal surface of the nasal organ. This gap is the result of the further resorption which just began in the last larval stage described. From its point of origin opposite the verticale in the planum tectale, resorption has extended anteriorly, laterally and posteriorly, until all that now remains of the complete cartilage roof is a slender bar of cartilage, the dorsal process of Winslow, uniting the anterior cupola with the lateral wall of the capsule. Posterior to the verticale, a narrow bar, a remnant of the ethmoidal column, passes over the foramen olfactorius and connects with the posterior tectale which now is reduced to a narrow band of cartilage. Lateral to the foramen orbitonasalis (*fon*) the tectale broadens slightly, and curving obliquely forward forms a partial roof over the choana and lateral parts of the nasal sac (Figs. 47, 48). More laterally this roof, better known as the lamina externa (*le*), is pierced by three foramina, for a blood vessel and two branches of the externus profundus nerves.

The caudal extension of the cornu trabeculae is more posterior than before, and a transverse section through the planum verticale shows the posterior end of the organ of Jacobson lying between the cornu and the lateral part of the tectale (Fig. 47). The fenestra infra-conchalis (*fen ic*) is more elongate and contains the anterior end of Jacobson's organ (Fig. 48, *jo*), which medially is partially covered by a part of the cartilage of the tectale which supports the naso-lacrimal duct. From this, a cylindrical bar of cartilage, the dorsal process, extends to the cupola, affording the only

covering to the nasal sac in this region, and which at the same time forms the medial boundary to the external naris. The small band of cartilage, which in the 45 mm. larva connected the tectale to the cornu trabeculae, persists as a flat plate separating the narial opening from the fenestra infraconchalis, and is pierced by a small foramen for the externus branch of the profundus nerve as it passes to the exterior.

Anterior to the planum verticale, a band-like cartilage, the lamina medialis (*lm*) continues forward to the cupola. It is pierced by a single large opening at the base of the prenasal process through which the nasalis internus of the profundus passes to the internasal space.

In the larva of Amblystoma there is, first, a progressive development which results in a well chondrified nasal capsule, reaching the extreme in the oldest larval stage. With the assumption of adult conditions and the more extensive development of bony structures, this capsule undergoes a marked reduction, chiefly by the resorption of parts. Evidently there is some relationship between the development of the cartilage capsule and the period of metamorphosis, the significance of which will be discussed later.

SALAMANDRA MACULATA

In a larva of *Salamandra maculata* 25 mm. long (Fig. 11), the nasal capsule has chondrified to a stage intermediate between that of the 25 mm. and 34 mm. Amblystomal larvae. The cristae trabeculorum (*cr t*) terminate abruptly just anterior to the region of the eye, from whence the trabeculae pass forward a short distance and then unite to form a broad trapezoidal planum basale (*pb*). The posterior margin of the planum is parallel to and one-half longer than the anterior, and bears a strong caudal process (*cp*), which Parker has called the hinder process, lacking in all other stages and in all Urodeles which I have studied, with the exception of a single stage of Cryptobranchus. The dorsal surface of the planum is more concave than that of the corresponding stage of Amblystoma and the ridges formed by the trabeculae are more prominent.

A broad trabecular cornu (*ct*) arises from the antero-lateral angle of the planum basale as a thin triangular cartilage, which supports the anterior part of the nasal sac. The lateral margin of each cornu is oblique to the axis of the skull and meets the posterior margin at the level of the anterior boundary of the planum basale; more medially the posterior margin curves backward and fuses with the lateral margin of the planum basale near its middle.

Parallel to each trabecula, and lying adjacent to the dorsal medial margin of each nasal sac, is the columna ethmoidalis (*ce*). In this stage of Salamandra, each ethmoidal column is united to the medial margin of the cornu, before the pons ethmoidalis appears; and this fact suggests that the columna does not arise independently here, but is a development back-

wards from the anterior cornu, just as in Spelerpes. At its posterior end a small process, the beginning of the planum tectale, extends laterally and then bends ventrally over the hinder end of the nasal sac at the level of the choana; this planum tectale arising here as in Amblystoma from an outgrowth from the columna ethmoidalis. A small groove between the anterior tip of the cornu trabeculae and the columna ethmoidalis allows for the passage of the nasalis internus branch of the profundus nerve to the internasal space (*ins*).

An antorbital process (*pa*) arises from the latero-ventral margin of each trabecula and extends laterally a short distance and anteriorly to a point in line with the caudal margin of the planum basale.

In a 38 mm. larva, the nasal capsule is similar in many ways to that of the 45 mm. Amblystoma. The capsule has doubled in size and chondrification has advanced in all parts, so that the olfactory organs are now more completely protected. Each crista trabeculae has united to the posterior end of the ethmoidal column, forming a lateral wall to the cavum cranii, interrupted only by an oval foramen olfactorius (*fo*) for the olfactory nerve.

The planum basale (*pb*) resembles that of the earlier stage, but has now completely lost the hinder process, so that the posterior margin is semicircularly excavate as in the 45 mm. Amblystoma.

In a manner similar to that of the 25 mm. Amblystoma, an ethmoidal bridge has formed uniting the columnae ethmoidales of the two sides. This represents the beginning of the planum verticale which in the later stage completely closes off the internasal space from the cavum cranii, now in continuity by means of the circular fenestra ethmoidalis (Fig. 51, *fen eth*). The dorsal surface of the rudimentary verticale is flat, continuous with the dorsal margins of the ethmoidal columns; its anterior margin bears a triangular cephalic process (*ce p*) projecting into the internasal space and partially covering the intermaxillary gland, so that a sagittal section of the verticale appears triangular.

A lateral chondrification from the entire length of the ethmoidal column now forms a broad planum tectale (*pt*), which covers the nasal organ throughout its entire length. Anteriorly the tectale has united with the tip of the cornu trabeculae, forming a complete cupola (*c*), which is continuous with the verticale and is pierced only by a single foramen for the nasalis internus of the profundus nerve. The lateral margin of the anterior part of the tectale is separated from the lateral margin of the cornu by the large oval narial opening, which lacks the deep fenestra narina of the corresponding stage of Amblystoma; but similar to Amblystoma, the posterior tectale unites by a small band of cartilage to the cornu, near its posterior prolongation, which supports the organ of Jacobson. The nasolacrimal duct passes over this bar and is formed from two branches, which come from the inner angle of the eye.

From the ventral surface of the anterior cupola (*c*), a small prenasal process arises near the foramen nasalis internus and extends downward a short distance into the enveloping tissue. The antorbital processes (*pa*) are much as before, but as yet do not meet the anterior part of the floor of the capsule.

There are some resemblances between the nasal capsules of the last larval Amblystoma (Fig. 9), and the third stage of Salamandra (Fig. 13). In both the planum basale and verticale are greatly reduced and the olfactory organs lie well anterior to the forebrain. Complete chondrification of the verticale in Salamandra has obliterated the fenestra ethmoidalis, so that internasal space and cavum cranii are no longer continuous. The anterior cephalic process (*ce p*) of the verticale is cylindrical and more elongate than before and extends forward nearly to the level of the base of the prenasal process. I have not observed this structure in any other Urodele.

Each antorbital process has grown forward beneath the lateral margin of the tectale, and has united to the caudal extension of the cornu, thus outlining two large fenestrae. Of these, the largest lies in the floor of the capsule and surrounds the choana; while the orbito-nasal foramen (*fon*) is posterior and lies between the posterior margin of the tectale and the processus antorbitalis. In this stage the lateral margin of the tectale has not united to the antorbital process, although they lie very close, so that no fenestra infra-conchalis exists; but Jacobson's organ lies between these parts as in Amblystoma.

The anterior dorsal surface of the tectale is pierced by four foramina, the medial three of which conduct rami of the nasalis internus of the profundus nerve from the capsule; its main branch passing to the foramen nasalis internus at the base of the prenasal process. The lateral and larger gap represents in Salamandra the beginning of resorption, which has been described in a corresponding stage of Amblystoma. Posteriorly the tectale is pierced by a small foramen for a branch of the profundus.

This stage of Salamandra is very similar to the last larval stage of Amblystoma, and also represents the culmination of larval development. Resorption has begun and the capsule of the adult would probably be conspicuously reduced by the growth of the covering bones. Salamandra differs from Amblystoma in the complete separation of the tectale from the antorbital, and the consequent absence of the fenestra infra-conchalis; however the approximation of these parts would suggest their connection in the adult. The ethmo-palatine of Parker is the antorbital process, and he says that in the adult it is very likely to fuse with the anterior parts of the capsule. Furthermore Parker has described in the adult the persistence of the prenasal processes and the median rostrum, and says that they seem to be the non-segmented rudiments of the paired and unpaired elements of the foremost visceral arch, whose splints are the premaxillaries. This

median rostrum is not present in any other Urodele, although prenasal processes do exist in almost all types. Parker's homologies are hardly borne out by our present knowledge.

TRITON CRISTATUS

The nasal capsule of *Triton cristatus* differs in several points from that of either Amblystoma or Salamandra. In the younger of the two larvae accessible (28 mm.), the chondrification of the capsule is far advanced and I know nothing, except by inference, of the earlier stages. At this stage (Fig. 16) the capsule is somewhat rectangular in outline, gradually tapering toward the anterior end. The cristae trabeculorum (*cr t*) are well developed and form with the trabeculae, the walls of the cavum cranii, pierced only at their anterior margins by the large circular olfactory foramina (*fo*).

Immediately in front of the crests, the trabeculae are united by a very short planum basale (*pb*), which supports the olfactory lobes and the posior part of the intermaxillary glands; the latter, in this form, extending backward beneath the anterior part of the brain. The planum basale in Triton is very much smaller than that of Amblystoma, and lies more posterior in respect to the other capsular parts. Dorsal to, and somewhat anterior to the planum basale is a bar of cartilage which unites the capsules of the two sides just in front of the olfactory foramina. This is the pons ethmoidalis (*pe*), and is developed by medial growths from the dorsal part of both capsules, much as in Amblystoma to which it bears a resemblance. Unlike Amblystoma, however, the pons is never united to the basale by the planum verticale; but throughout life it is separated from it by a large circular fenestra ethmoidalis (*fen eth*) so that internasal space and cavum cranii are separated from each other by membranous structures only.

In contrast to the larval stages of most other Urodeles, the nasal organs of Triton are almost entirely anterior to the forebrain, so that planum basale and pons ethmoidalis are close to the posterior parts of the capsule. As a result of the relation of the central nervous system to the nasal structures, each capsule appears as a segment of an elongate cone, obliquely truncate anteriorly, with the anterior half of its lateral wall interrupted by a very large narial opening. As is true for all Urodeles, the cartilage structures of each side, in front of the planum basale, are separated by an internasal space (the intermaxillary room of Born, 1877). which in Triton is more elongate and extends between the walls of the anterior two-thirds of the capsule.

Anterior to its junction with the crista trabeculae, each planum tectale (*pt*) curves outward and downward, completely covering the posterior parts of the nasal sac and the choana; laterally it continues into the lamina externa which covers the posterior part of the organ of Jacobson. More posteriorly, each lamina externa has united to the anterior prolongation of

the antorbital process, thus completing the foramen orbito-nasalis (*fon*) through which the nerves of the nasal region enter the capsule. A small foramen in the tectale, just opposite the pons ethmoidalis conducts a branch of the profundus nerve from the capsule; while the larger oval gap in the anterior tectale, separated from the external naris by a narrow bar is one of the gaps described by Born in the adult.

The lamina medialis (*lm*) forms the medial wall of the capsule, anterior to the foramen olfactorius, and is continuous with the tectale and the cornu trabeculae (Fig. 56), thus bounding the internasal space. The floor of the capsule is formed by a large trapezoidal cornu trabeculae which extends back to the level of the pons ethmoidalis where it forms the anterior margin of the choana. Its lateral margin unites to the lamina externa, forming the boundary to the naris, over which the naso-lacrimal duct passes to the nasal sac, as in Amblystoma and Salamandra. Posterior to its junction with the lamina externa, each cornu terminates in a small posteriorly-directed process, which supports the organ of Jacobson; although, as in Salamandra, a fenestra infra conchalis does not yet exist. At the anterior end, the floors of the two capsules approach each other, and at the extreme medial tip of each is a small prenasal process (*pnp*), probably the homologue of that structure in both Amblystoma and Salamandra. The nasalis internus of the profundus nerve leaves the capsule through the foramen at the base of the prenasal process.

The nasal capsule of the older larva of *Triton cristatus* (35 mm. long) is intermediate between the 28 mm. stage and that described by Born (1877), in which large gaps have developed. In this stage there has been a reduction in the length of the capsule, most of which occurs at the anterior end, so that the width is greater in proportion to the length than in the earlier larva. The relation of the forebrain to the nasal sac is much as before; but in the adult, according to Born, all olfactory structures are entirely anterior to the central nervous system. The planum basale and the pons ethmoidalis are much as in the earlier stage, except that the pons is now much farther anterior than is the basale, while the foramen olfactorius and ethmoidalis are larger than before (Fig. 17).

Cartilage has formed around the branch of the profundus nerve which supplies the organ of Jacobson, cutting off a smaller foramen adjacent to the foramen orbito-nasalis (Fig. 17, 57). Just anterior, and slightly lateral to this foramen, the lamina externa has united to the caudal extension of the cornu trabeculae thus outlining the foramen infra-conchalis, as in Amblystoma, through which the organ of Jacobson protrudes from the capsule.

Further description of this capsule is unnecessary, with the exception of the cupola (*c*), which now encloses the anterior parts of the nasal sac, so that now the external naris is entirely lateral. The lamina medialis (*lm*)

is pierced by a small foramen for a branch of the nasalis internus of the profundus nerve, the main part of which leaves the capsule through the foramen in front of, and at the base of the prenasal process. At the anterior end of the floor of the capsule is a small gap which I believe to be the beginning of the larger gap described by Born for the adult.

It is impossible to be certain of all the homologies between the nasal capsule of Triton and that of Amblystoma, without the early stages. Born (1877) has described the process of chondrification, but has shown no figures for his early stages. Terry (1906) says: "The development of the cartilaginous nasal skeleton of Amblystoma is comparable in many respects with the processes in Triton as described by Born." Born says nothing of an ethmoidal column which chondrifies independently and then later becomes associated with the trabecula; on the contrary he says: "Bei den Tritonen die Knorpelkapseln der Nasenhöhlen durch directes auswachsen der Trabecel gebildet werden." The lamina medialis, planum tectale and lamina externa would thus be formed by a continuous growth from the trabecula; while the many gaps in the capsule would arise by interruptions in the process.

Throughout its development, Amblystoma never has a fenestra ethmoidalis completely outlined, and yet it is distinctly present in both stages of Triton; and Born says: "Dieser Internasalraum ist bei Triton cristatus und taeniatus, niemals durch eine knorpelige Wand von der Schädelhöhle geschieden, sondern immer hautig gegen dieselbe abgeschlossen."

In larvae of Salamandra, Pelobates and Rana, the fenestra ethmoidalis is complete, being bounded by cartilage upon all sides, but is closed in the adult; while it persists throughout life in Triton and Diemictylus.

DIEMICTYLUS VIRIDESCENS

The nasal capsule of a 38 mm. larva of *Diemictylus viridescens* resembles in many ways that of the 35 mm. *Triton cristatus*. In both, the two capsules are united by a very small planum basale, the only connection between them even in the adult Diemictylus, which lacks the pons ethmoidalis; so that internasal space and cavum cranii are continuous cavities. The small planum basale (*pb*) supports the anterior part of the telencephalon which reaches forward into the internasal space; so that olfactory lobes and intermaxillary glands overlap in this animal (Figs. 14, 53).

The antorbital process (*pa*) has united to the posterior margin of the tectale at two places, thus outlining two small fenestrae the inner of which is the foramen orbito-nasalis (*f o n*) for the nasalis internus of the profundus nerve; while the outer conducts the externus branch of the profundus, which supplies Jacobson's organ.

Anterior to these foramina, the united elements of the planum tectale and the antorbital process completely cover the dorsal and lateral parts of

the olfactory organ; and together with the posterior prolongation of the cornu form a shelf upon which the posterior parts of Jacobson's organ rest. Slightly anterior to its junction with the cornu, the tectale is pierced by a small circular foramen, which, like the infra-conchalis of Amblystoma and Triton, contains the anterior end of the organ of Jacobson. The planum tectale is interrupted on its anterior half by two oval openings, of which the external naris is the larger, extending back nearly to the middle of the capsule. The more medial gap is much smaller and marks the beginning of the process of resorption, just as in the older Triton larva.

The lamina medialis (*lm*) is continuous with the tectale and forms the medial wall of the capsule from the planum basale to the anterior cupola; while ventrally, it curves into the floor of the capsule which is pierced by two small foramina, through which rami of the nasalis internus nerve leave the capsule. The main branch of this nerve passes to the internasal space through the larger foramen just in front of the base of the pre-nasal process.

The adult Diemictylus (Fig. 15) shows no further chondrification of structures than those present in the larva. Ossification has taken place in all parts and further resorption has increased the size of the gaps present in the earlier stage. A single foramen exists above the antorbital process, so that both nasalis internus and externus of the profundus nerve enter the capsule through the foramen orbito-nasalis.

The planum tectale is more vaulted than before, and its posterior half is pierced by two foramina; the medial of which is for a branch of the profundus nerve, while the lateral and larger one contains, as before, the cephalic end of Jacobson's organ. The anterior tectale has two large openings, the external naris, lateral in position, and, medial to this, the further development of the gap begun by resorptive processes of the larva.

The ventral surface of the adult capsule has a greatly enlarged choana, which occupies the posterior two-thirds of the floor. It is bounded laterally by the prolongation of the cornu, which in this stage extends beyond the junction to the tectale, so that a short process, behind the shelf, supports the posterior parts of the organ of Jacobson. The anterior part of the floor and the cupola need no description, further than the mention of five small foramina for branches of the nasalis internus nerve.

The nasal capsules of Triton and Diemictylus are very close. The presence of the same large gaps, and the reduced planum basale, together with the continuity of cavum cranii with the internasal space are strong resemblances between the two. The fenestra ethmoidalis is not a permanent character of any other adult, although it is temporary in some larvae as Salamandra and certain Anura. There are some resemblances between the capsules of the adult Amblystoma and Diemictylus. In both, the anterior part of the organ of Jacobson extends through a foramen which in

Amblystoma is called the infra-conchalis, separated from the naris by a cartilage bar; while the posterior part of Jacobson's organ rests upon a shelf formed by the prolongation of the cornu. The orbito-nasal foramen, the choanal opening, and the relation of the olfactory organ to the capsule, are features common to both Amblystoma and Diemictylus; and yet the absence of a planum verticale, the greatly reduced planum basale and the complete continuity of internasal space with cavum cranii in the latter form, preclude the determination of close relationships here.

CRYPTOBRANCHUS ALLEGHANIENSIS

Practically no work has been done upon the development of the skeleton in the larval stages of Cryptobranchus, although the adult skull and nasal structures have been described by Parker (1876), Wiedersheim (1877), and Wilder (1892). I have studied four stages in the chondrification of the nasal capsule, and although my material lacks some intermediate steps in the process, yet I am able to recognize the method of development and to note some features that may prove interesting from a phylogenetic point of view.

The early process of chondrification in Cryptobranchus is similar to that in Amblystoma, and my earliest stage suggests the eleven mm. larva of that animal with certain additional features. In a larval Cryptobranchus two weeks after hatching (Fig. 22), a nasal capsule has not yet formed. The cristae trabeculorum (*cr t*) are very strong and high, but terminate abruptly near the anterior margin of the eye; while the trabeculae continue anteriorly, turning slightly medially but not meeting to form the planum basale. Each is curved upon its medial surface, which rests against the olfactory lobe; while anteriorly a ventral lateral expansion of the trabecula is the beginning of the cornu (*ct*), which resembles Amblystoma, and ends in a blunt process in the surrounding tissue.

In contrast to the eleven mm. Amblystomal larva, trabecular crests are well developed in this stage of Cryptobranchus; while on the other hand, the cornua trabeculorum which are well developed in the young Amblystoma are just beginning to chondrify in Cryptobranchus. Antorbital processes have not formed, nor is there any trace of an ethmoidal column as in the youngest Amblystoma.

In a larva five weeks after hatching (Fig. 23), chondrification has advanced in all parts, but the absence of an intermediate stage prevents a definite conclusion as to the origin of certain structures. In general the capsule resembles in many respects that of the 25 mm. Salamandra.

From the anterior end of the crista, each trabecula inclines toward the median line for a short distance, and then passes straight forward and is united with its mate by a small planum basale (*pb*) similar in size to that in *Triton cristatus*. This planum basale differs from that of any Urodele thus

far described, in the fact that the dorsal surface is not concave but is convex and bears upon its anterior half a distinct median swelling which probably is the beginning of a planum verticale (Fig. 58). The anterior surface is straight and at right angles to the median surface of the skull, while the posterior possesses a short caudal process similar to that in the 25 mm. Salamandra larva.

Anterior to the planum basale, each trabecula extends forward a short distance and from its medial margin a columna ethmoidalis (*ce*) arises dorsally as a broad band of cartilage, partially separating the anterior part of the nasal sac from the internasal space. Passing backwards, upwards and outwards along the dorsal medial side of the olfactory organ, each column becomes more rod-like; and at the level of the anterior margin of the planum basale it expands into a large rhomboidal plate, the planum tectale (*pt*) which extends forwards and outwards, covering the dorsal and lateral parts of the nasal sac. Each tectale is pierced by a small foramen through which a branch of the profundus nerve passes from the capsule. Posterior to the tectale, each column continues backward and unites to the crista trabeculae.

The cornu trabeculae (*ct*) of Cryptobranchus differs from that of any other Urodele. In contrast to the board triangular plate of both Amblystoma and Salamandra, it is reduced to a narrow bar, which curves backwards and upwards from the lateral anterior margin of the trabecula to a point just below the tectale, to which it fuses in a later stage. A small notch at the anterior end of the capsule, between the ethmoidal column and the cornu allows for the passage of the nasalis internus nerve to the internasal space.

From each trabecula, just posterior to the large foramen olfactorius, a slender process passes laterally a distance equal to the width of the trabecula, and then bends abruptly to pass backward to the pterygo-quadrate, while it utterly lacks any anterior prolongation. The morphological relations of this bar will be discussed in connection with a later stage.

In a larva two months after hatching, a more complete capsule has formed. The planum basale has lost the hinder process and is now continuous with the planum verticale, which unites the two capsules just anterior to the oval olfactory foramina and completely separates the cavum cranii from the internasal space. Anterior to the verticale, the columna ethmoidalis and cornu trabeculae have expanded to form the lamina medialis covering the entire medial surface of the nasal organ. A notch, marking the junction of column and cornu, allows for the passage of a branch of the nasalis internus to the internasal space.

The planum tectale is considerably larger than before, reaching back to the crista and extending forward over the posterior tip of the cornu trabeculae, with which it is not yet united. It is pierced by a small foramen as

in the earlier stage. A wide bay, the fenestra narina, marks the anterior boundary of the tectale, and here, as in Amblystoma, is a larval character, disappearing in the adult. The cornu trabeculae is somewhat wider than before, although differing considerably from the broader cornua of other Urodeles. A small notch at the anterior end of the cornu conducts a second branch of the nasalis internus from the capsule.

In the last stage of Cryptobranchus studied, a larva three months old (Fig. 24), chondrification has advanced in all parts, forming a well-defined nasal capsule, resembling in some respects the 45 mm. Amblystoma. The planum basale and verticale are much as before, supporting the olfactory lobes, and uniting the capsules of the two sides just anterior to the olfactory foramina. Anterior to the planum verticale, the lamina medialis (*lm*) formed by both ethmoidal column and trabecula, together with the cornu forms the anterior cupola of the capsule, which is pierced by two foramina, one medial and the other ventral, through which the branches of the nasalis internus nerve leave the capsule. The olfactory duct continues forward beyond the lateral margin of the cupola and opens through the external naris, anterior to all capsular structures.

The cornu trabeculae is much as in the earlier stage, except that it has now united to the anterior extension of the planum tectale, just as in all other Urodeles thus far described; and the organ of Jacobson rests upon the caudal extension of the cornu behind this connection. The tectale itself is larger than before, reaching forward a short distance beyond its junction with the cornu, thus completely covering the choana and the dorsal parts of the nasal sac. The fenestra narina is deeper than before, extending back from the naris to the planum verticale. A branch of the superficialis nerve enters and leaves the capsule through this bay; but in a later stage, cartilage has chondrified around these nerves leaving two small foramina, and completely obliterating the narina, as in the last larval stage of Amblystoma.

In this stage, the bar of cartilage mentioned in connection wth the five weeks larva as extending at right angles from the side of the trabecula, has attained such relations as to throw light upon its morphology. At its tip it is directly connected with the anterior end of the pterygoquadrate bar, which extends back to the otic region where the relations are much the same as in all Urodeles. This completeness of connection of the pterygoquadrate with the anterior parts of the trabecula is paralleled, so far as I know, only in the Siberian genus Ranodon (Wiedersheim 1877, Fig. 69), and is lost in the adult of Cryptobranchus, both our species and the Japanese japonicus.

Some years ago, Gaupp questioned a statement by Kingsley (1892, p. 672), who said: "the lower process may retain the name 'antorbital', usually applied to it, for Amphiuma presents no evidence that it is the

palatine cartilage as Gaupp interprets it." Gaupp (1893, footnote p. 430) says: "Hierzu möchte ich bemerken, dass ich die beiden Namen 'Antorbital-fortsatz' und 'Cartilago palatina' durchaus für dasselbe Gebilde gebraucht habe (17, p. 115: 'die Cartilago palatina' oder wie die englischen Autoren Huxley und Parker den Knorpel nennen, den 'Processus antorbitalis'). Als 'Processus palatinus' wird der Knorpel aber z.B. von Friedreich und Gegenbaur bezeichnet (14, p. 29), auch Hertwig (24) nennt ihn auf den Figuren 'Cartilago palatina' (C.p.), und Wiedersheim (58, p. 483) spricht von einen Antorbitalfortsatz oder 'Gaumenfortsatz' der deutschen Autoren. Da ich beide Bezeichnungen in der Literatur vorfand, so erwähnte ich sie auch beide, habe aber nicht etwa einem bekannten Gebilde eine neue Deutung geben wollen. Kingsley scheint unter 'Palatine cartilage' hier etwas Besonderes zu verstehen; was das ist, kann ich aus seinen Angaben nicht ersehen."

Winslow (1898) discussed the question, and concluded that until it was shown that the process in Urodeles arising from the trabecula in front of the orbit was actually a part of the pterygoquadrate the name antorbital should be retained. A further point is that the term palatine cartilage is misleading, implying that it is the rudiment of the palatine bone, which is not cartilaginous in origin.

With the evidence now presented by Cryptobranchus, it would seem as if the basal part of the process here, and by implication in all Urodeles, is really an anterior prolongation of the pterygoquadrate. But the anterior portion of this process is something additional, and although possibly pterygoidal in origin, may retain the name antorbital. Then in all other groups, where the posterior connection to the quadrate is lost, the entire outgrowth, although partly pterygoidal, is best known as the antorbital process. Of course this retention of the anterior part of the pterygoid in both Cryptobranchus and Ranodon larvae is an ancestral feature lost elsewhere among the Urodeles. As stated in the above, the adults of both species of Cryptobranchus have lost the connection of the pterygoid with the side of the cranial wall, and in both the direction of the posterior plainly pterygoidal part of the cartilage would not suggest that in the larva there was any such connection with the trabecula or any relation with the palatine bone.

Of the Urodeles thus far described, Cryptobranchus stands alone in the origin of the planum verticale, which arises as a medial dorsal growth from the planum basale, subsequently uniting to the medial margins of the columnae ethmoidales and closing off the cavum cranii from the internasal space. Thus at no time does a pons ethmoidalis or a fenestra ethmoidalis exist in Cryptobranchus, like that in Amblystoma and Salamandra. On the other hand the columna ethmoidalis in Cryptobranchus recalls that structure in Salamandra which, arising in both from the medial margin of

the cornu, grows posteriorly along the nasal sac. Unlike Salamandra, however, the planum tectale does not develop from the posterior end of the ethmoidal column, but rather chondrifies laterally from about its middle.

Although the planum tectale and the anterior cupola of my later stage resembles in some ways those of both Salamandra and Amblystoma yet the large planum basale and cornu trabeculae of the latter forms, do not exist at any time in Cryptobranchus, both of these structures being greatly reduced.

SPELERPES BILINEATUS

The nasal capsule of a Spelerpes larva 15 mm. long (Fig. 18) differs but little from those of the early stages of all Urodeles. The trabeculae (*t*) are more cylindrical than in Amblystoma, however, and extend forward to the tip of the forebrain, not meeting as yet to form the planum basale. At their anterior ends, each trabecula expands into a triangular cornu, considerably smaller than the cornua of corresponding stages of Amblystoma, and, which only partially supports the anterior part of the nasal organ (Fig. 59). Ethmoidal column nor crista trabeculae have not appeared in this stage.

In a 37 mm. larva (Fig. 19) other parts of the capsule have chondrified, but on the whole the capsule is far more simple than any other Urodele of that age. The cristae trabeculorum (*cr t*) are well developed and together with the trabeculae form the walls of the cavum cranii. Each crista terminates at the level of the antorbital process, and from its dorsal margin a short process extends anteriorly, which appears to be associated with the development of the ethmoidal column, as described in the later stage.

From its junction with the crista, each trabecula inclines toward the median line and is united with its mate by a small planum basale (*pb*), convex upon its dorsal surface and resembling this structure in the second stage of Cryptobranchus. Just anterior to the planum basale the trabeculae are strongly concave and a prominent ridge has developed along their medial margins, forming a groove for the branches of the nasalis internus of the profundus nerve (Fig. 60). The trabecular cornu is well developed in this stage; its posterior margin extending backwards as a short process to the level of the anterior margin of the planum basale.

The antorbital processes (*pa*) are much as in others of the order, arising from the trabecula just beneath the crista, extending laterally a short distance, and then bending anteriorly toward the capsule.

My oldest stage of Spelerpes is a larva 46 mm. long (Fig. 20). Some additional structures are present, but the capsule is not completely developed and satisfactory comparisons with the capsules of other Urodeles can not be made.

Opposite the eye, the cristae trabeculorum (*cr t*) are low; but farther forwards they are higher, their anterior ends being free from the lower

trabecula and reaching farther forward than before (Fig. 21). Anterior to the crista, each trabecula turns more abruptly toward the median line for a short distance, and then anteriorly; uniting by a very small planum basale, which in this stage is flat and level, with the dorsal surfaces of the trabeculae.

Anterior to the planum basale, the trabeculae continue forward, separated from each other by a narrow internasal space; each expands distally into a small cornu which supports the tip of the nasal organ. Arising from the dorsal and medial margin of each trabecula, just anterior to the planum basale, is a small process which extends backward a short distance along the medial margin of the nasal sac. This process is the further development of the medial ridge of the trabecula in the 37 mm. stage; and from its relation to the nasal organ, it must be the beginning of the columna ethmoidalis, whose further history is unknown (Fig. 61).

I regret that I have no older stages showing the farther chondrification of the capsule; thus preventing a careful comparison with other Urodeles. In general, however, Spelerpes seems to indicate a retarded growth in all parts. In corresponding ages of other Urodeles, there is a much more complete capsule than in Spelerpes.

I have not observed the free anterior extension of the crista in any other Urodele, with the exception of Amphiuma; and judging from its relation to the nasal organ and trabecula, it would appear as though this process is the posterior beginning of the ethmoidal column. In other words the columna ethmoidalis in Spelerpes may arise by the fusion of two parts independent of each other; the anterior part from the medial margin of the cornu, the posterior part from the anterior margin of the crista. In no other Urodele, as far as I have seen, does the column arise in just this way; however the early development of the crista trabeculae in Cryptobranchus and the lateral development of the tectale from the middle of the ethmoidal column, leads me to conclude that in Cryptobranchus the column arises, as in Spelerpes, from two distinct independent outgrowths.

The small planum basale is similar to that in Cryptobranchus, but the larger cornu in the 37 mm. stage is more like that of Amblystoma. My material does not show the formation of the planum verticale, but it evidently does not arise as a dorsal growth from the planum basale, but more probably by medial growths from the ethmoidal columns; thus in this particular, approaching the condition in Salamandra.

The complete absence of intermaxillary glands, the close approximation of the capsules anterior to the planum basale, as well as the small size of the latter, are points of similarity to Cryptobranchus, which, on the evidence of larval characters alone, I believe Spelerpes more closely resembles.

PLETHODON ERYTHRONOTUS

Winslow (1898) has described the nasal capsule of a 20 mm. larva of *Plethodon glutinosus*, and he compares it with a 45 mm. Amblystoma. I have not studied any larval form of this genus, but have examined and modelled the capsule of an adult, which is similar in many respects to my last stage of Amblystoma. In the adult, ossification is extensive and in some parts, all traces of a chondrocranium have disappeared. This is especially true in the region of the eye, where the trabecular crests have disappeared as far forward as the olfactory foramina, so that these openings are confluent with the foramina orbito-nasales in this stage (Fig. 27).

The dorsal surface of the nasal organ is exposed throughout its entire length by a large gap in the capsule, similar to that of the adult Amblystoma; so that the planum tectale is reduced to a small cartilage plate covering the posterior end of the nasal sac behind the choana. The lamina externa (*le*) formed by elements of the tectale and processus antorbitalis, passes obliquely forward as a band of cartilage, protecting the lateral parts of the nasal sac and the organ of Jacobson (Fig. 62). The nasalis externus of the profundus nerve enters the capsule through a small foramen in this plate, and is partly distributed to Jacobson's organ; while the main branch of the nerve leaves the capsule through the foramen in the more anterior part of the capsule. Just lateral to the foramen nasalis externus (*fne*), the lamina externa abruptly expands from its ventral margin into a horizontal plate which partly covers Jacobson's organ, its lateral angle terminating in a small anterior process; while more anteriorly it narrows considerably and lies directly above the posterior prolongation of the cornu (Fig. 63). The anterior medial angle of the lamina externa is united by a cylindrical bar to the anterior cupola, as in the adult Amblystoma (Fig. 10), which separates the external naris from the large gap in the dorsal surface. The naso-lacrimal duct passes to the nasal organ through the notch between this bar and the anterior part of the externa, which is pierced by the foramen for the exit of the nasalis externus, as mentioned above.

The floor of the capsule is formed by the cornu trabeculae, which has united to the lateral margin of the lamina externa, and continues posteriorly as a short process supporting the anterior end of the organ of Jacobson. The ventral gap in the capsule is very large and is similar to that in Amblystoma.

The planum basale and verticale are united throughout their entire length, forming a thick plate which unites the capsules just anterior to the olfactory foramina and separates the internasal space from the cavum cranii. Anterior to these parts, the lamina medialis (*lm*) forms the medial wall of the capsule; narrower at its junction to the verticale, it becomes wider more anteriorly and finally uniting with the cornu trabeculae, it forms the anterior vault of the capsule. Midway between the tip of the capsule

and the verticale, the lamina medialis is pierced by two foramina, through the dorsal of which, the nasalis internus of the profundus nerve passes to the intermaxillary gland; while a blood vessel passes through the more ventral one. A small prenasal process extends anteriorly a short distance from the median ventral surface of the cupola. The internasal space is deep and narrow, and it is filled with intermaxillary glands which extend back beneath the planum basale, to its posterior margin. In the presence of these glands, Plethodon differs from Cryptobranchus and Spelerpes but resembles Amblystoma and Salamandra.

In all essentials Plethodon resembles very closely the adult Amblystoma to which it is probably nearly related. The absence of earlier stages has prevented a study of the development of the capsule; but comparing the single larval stage of Winslow with my early stages of Amblystoma, coupled with the many resemblances between the adults, I am inclined to place Plethodon very near to Amblystoma. The absence of the fenestra infra-conchalis in Plethodon is the primary difference between these capsules; but the position and size of the planum verticale, the lamina externa and medialis, the anterior cupola as well as the large dorsal and ventral gaps are resemblances that suggest a very close relationship between these animals.

NECTURUS MACULATUS

As in Spelerpes, the chondrification of the nasal capsule of Necturus is greatly retarded; so that, except for the mere extension of the trabeculae into the head region, there is no evidence of a nasal skeleton up to the 25 mm. stage. In higher Urodeles of this size, well developed capsules are already chondrified.

In a 24 mm. larva, the trabecular crests are not developed, and the cylindrical trabeculae incline toward each other, but do not unite to form the planum basale. There is no evidence of a cornu at the anterior end, nor has the antorbital process yet chondrified; but procartilage cells have formed near the trabecula which indicate its later development. The forebrain lies lateral to the nasal sac and extends slightly anterior to the trabeculae.

In a slightly older stage (Fig. 25), the anterior ends of the trabeculae more closely approach each other and near the tips they have expanded dorso-laterally, so that a cross section of the trabecula in this region is reniform. Miss Platt (1897) has described the independent chondrification of the planum basale, and its subsequent connection to the trabecula; although this stage does not show the chondrified basale, yet a few procartilage cells lying in the tissue between the anterior ends of the trabeculae indicate its origin as independent of the trabeculae. In this stage also, a small triangular antorbital process has chondrified from the trabecula.

In a 30 mm. larva (Fig. 26), some additional structures are present, although the capsule differs considerably from any other Urodele. The trabeculae are now united near their anterior ends by a planum basale (*pb*), trapezoidal in outline, its posterior margin being one and one-half times the length of the anterior. A median swelling upon the dorsal surface of the planum basale, together with the trabecular thickenings give the plate a bi-concave appearance, the olfactory lobes resting in the concavities. This median swelling, more evident over the anterior half of the planum and which resembles a similar structure in Cryptobranchus, must be regarded as a rudimentary planum verticale, although the later stage shows no further development of it (Fig. 64). Anterior to the planum basale, the trabeculae continue forward a short distance; and, without expanding into cornua so typical of other Urodeles, each trabecula, separated from its mate by a wide internasal space, ends bluntly in the surrounding tissue.

The beginning of the well-known fenestrated capsule of the adult Necturus, covering the nasal organs, mentioned and figured by Wiedersheim (1877) and others, appears in this stage. Directly over the medial margin of the nasal sac, and some distance from the trabecula is a small bar of cartilage, the columna ethmoidalis (*ce*), which extends from a little in front of the level of the anterior end of the trabecula back to the level of the posterior margin of the planum basale. At no time is it united to the trabeculae, and it recalls in origin and position this column in Amblystoma. A more posterior extension of this bar in the 33 mm. and 35 mm. stages, in which it reaches nearly to the antorbital process, suggests that here, as throughout the order, this bar chondrifies, first in the anterior parts and then develops posteriorly; although here it never unites to a crista trabecula, a structure entirely lacking in Necturus. Also in the 33 mm. and 35 mm. larvae I have observed cartilage cells along the lateral margin of the nasal sac, some of which lie between the folds of the nasal epithelium. These several areas do not seem to arise as a continuum, but chondrify independently and later become connected to each other and to the ethmoidal column to form the roof of the fenestrated capsule.

The antorbital processes are now more like those of other Urodeles, reaching forward a short distance toward the other parts of the capsule.

In the last stage of Necturus studied, a larva 45 mm. long (Fig. 28), the fenestrated nasal capsule (*fen pr*) has developed and resembles that of the adult. The trabecula (*t*), planum basale, and anterior extensions of the trabeculae are much as before, differing only in size; while the planum verticale, earlier prominent as the median ridge on the basale, is now reduced to a small swelling on the anterior half of the basal plate. Accordingly, the posterior half of the basale, which supports the olfactory lobes, is slightly and broadly concave.

The entire dorsal surface of the simple nasal sac and part of the lateral surface is covered by a curved and fenestrated cartilage, more extensive posteriorly where it curves ventrally over the choana. This process is a further development from the columna ethmoidalis with large additions from the cartilage cells described in the earlier stage, which now have united to each other in such a way that small gaps expose the dorsal surface of the nasal sac (Fig. 65). In front, the lateral parts of the fenestrated process are lacking, so that the ethmoidal column alone forms the roof in this region; while the more extensive chondrification occurs in the posterior parts. This more complete development posteriorly, and the gradual reduction toward the anterior end culminating in the unspecialized ethmoidal column, indicates a development from behind forwards, and recalls the condition in both Salamandra and Amblystoma in which the columna ethmoidalis develops lateral processes, first from its posterior parts. Although the fenestrated process of Necturus never unites to other capsular parts, yet because of its relation to the ethmoidal column and the nasal organ, it is the homologue of the planum tectale of other Urodeles.

The antorbital processes (*pa*) are larger than before, and although they lie near the lateral parts of the fenestrated tectale, the two never unite, so that a foramen orbito-nasalis is never completely enclosed; nor is there any circumscribed olfactory foramen since the column is completely distinct from the trabecula, and the olfactory nerve passes between column and trabecula to the olfactory organ.

The early development of the nasal capsule of Necturus resembles that of other Urodeles to this extent; the trabeculae with their antorbital processes, the planum basale and the ethmoidal columns are common to all. On the other hand, Necturus lacks the characteristic expanded cornua, the trabeculae ending bluntly, as well as a planum verticale and lamina medialis, which in all other Urodeles completely separates the nasal organs from each other and closes the internasal space from the cavity of the forebrain. The nasal organs of Necturus are exposed on their ventral, medial and lateral surfaces, and are only incompletely covered on the dorsal by the fenestrated cartilage. In the origin of the columna ethmoidalis and its subsequent direction of growth, together with the development of the fenestrated roof, there is a similarity to Amblystoma; but the many striking contrasts between the capsules of these two Urodeles must establish very remote relationships between them, or are possibly to be interpreted by the neotenic character of this animal.

The lack of skeletal protection for the nasal organs, the absence of many parts of a typical urodelan capsule, as well as the very unspecialized nasal sac itself, suggests for Necturus that it is to be regarded as either ancestral, as a permanent larva or as indicating degeneracy of parts. To regard Necturus with its fenestrated capsule, which has no counterpart

throughout the entire urodelan order, as primitive, would be unjustified; but, the greatly retarded process of chondrification, the absence of cristae and cornua trabeculorum, together with the entire separation of the roof of the capsule from the other parts, may be explained in either of two ways; Necturus has either descended from some more specialized Urodele, or, as the retarded process of chondrification would suggest, it may represent a neotenic condition of some form, like Spelerpes.

AMPHIUMA MEANS

The first of the three capsules of Amphiuma studied, is that of a larva still within the egg, in which the chondrocranium is very incomplete, resembling in many ways the larva described by Kingsley (1892), and figured by Winslow (Fig. 18, 1898).

Each trabecula, from the crista forwards, inclines, at first gradually, and then somewhat more abrupt, toward the median line; the two uniting to form a small rectangular planum basale (*pb*, Fig. 29), which supports the olfactory lobes. Anterior to the planum, each trabecula continues forward a short distance, and then expands into a triangular cornu, concave upon its dorsal surface to support the anterior part of the olfactory sac. The cornua are separated from each other by a deep and narrow internasal space, resembling that of Spelerpes, the Urodele, the larva of which most resembles the early Amphiuma.

The cristae trabeculorum (*cr t*) are well developed and extend forward to the base of the antorbital process (*pa*), which in Amphiuma is directed obliquely forward from the trabecula, rather than at right angles to it as in other Urodeles. The anterior margin of each crista trabeculae is continued forward as a cylindrical bar along the medial dorsal margin of the nasal sac. At the level of the anterior end of the antorbital process, the bar runs forward and outward and passes obliquely over the nasal organ, giving rise to a short process just dorsal to the nasal sac, and continuing outward and downward to the lateral surface of the sac where it turns directly forward and runs along the lateral surface of the sac nearly to the level of the planum basale. Hay (1890) speaks of this bar as the rudimentary nasal capsule, while Winslow (1898) describes it as projecting forward, outward and downward, but without the small dorsal processes present in my stage, and which help to explain the later modifications of the capsule. In its origin from the trabecular crest, this bar, which probably contains elements of both ethmoidal column and tectal cartilage, recalls the process in Spelerpes, extending forward from the anterior margin of the crest, which was interpreted as the posterior end of a developing columna ethmoidalis.

Olfactory foramina do not exist, but each olfactory nerve passes over the trabecula just in front of the crista trabeculae, where the nasal organ and the olfactory lobe are very close together.

In an older larva, a more complete nasal capsule (Fig. 30) has been formed, which resembles in but few respects those of other Urodeles. It is somewhat ovoid in outline, its greatest width being about one-fifth its length. From the anterior end of the crista, each trabecula, relatively more slender than before, inclines medially and passing along the lower margin of the olfactory lobe, unites with its fellow at about the level of the middle of the capsule, to form the planum basale (*pb*). This plate is considerably larger than before, and together with the cornu of either side, forms a plate roughly hexagonal in outline. Its posterior margin is straight, while lateral to the line of the trabecula, its caudal margin is directed antero-laterally to a point corresponding to the lateral angle of the cornu of the early stage, where it fuses with another cartilage bar yet to be described. Each lateral-cephalic margin is also curved and is produced in front, in a line with the trabecula, into a process directed forward from the planum, the anterior extension of the trabecula. These cornual tips are separated by an internasal space somewhat wider although much shorter than before.

The planum verticale (*pv*) arises from the anterior half of the basale, just back of the internasal space, as a narrow band of cartilage, which separates the nasal organs in this region (Fig. 69, *pv*). Dorsally the planum verticale divides into two bars, the alary processes, which are inclined to each other at about an angle of 60 degrees. Each alary process is continuous with the columna ethmoidalis, and partially covers the antero-median surface of the olfactory sac.

The columna ethmoidalis is now complete, extending forward from the crista to, and slightly beyond, the alary process. Apparently this corresponds to the bar arising from the superior margin of the crista of the earlier stage, as far as and including the small process dorsal to the nasal sac described above. The more lateral portion of the earlier bar is evidently the lamina externa of this stage, which now extends forwards along the lateral surface of the nasal organ. At about the level of the planum verticale, the lamina externa (*le*) sends a process downwards, which unites with the lateral angle of the cornu. The lamina externa continues beyond this junction as a broader plate, ending in an oblique circumnarial cartilage ring surrounding the narial aperture.

The antorbital process is much as before, being inclined at an angle of about 30 degrees from the trabecula, rather than at right angles to it as in most other Urodeles.

Many of the characters of the nasal capsule of the adult Amphiuma, as described by Wilder (1892), appear in a larva 82 mm. long. The nasal capsule (Fig. 31) has doubled in size, although the proportions are unchanged; additional chondrification having occurred in the anterior parts. The crista trabeculae, antorbital process, trabecula, planum basale, and

columna ethmoidalis are much as in the younger stage, and need no further description. The dorsal surface of the capsule, however, has been changed by the continuation forward of the ethmoidal column to a junction with the circumnarial cartilage and a lateral extension of the cartilage from the column to the lamina externa; so that the whole anterior end of the capsule is roofed in as far back as the level of the verticale, this roof being perforated behind and near its median line for the passage of the nasalis internus of the profundus. The lamina externa, behind its connection with the cornu is wider than before, and close to the lower margin near its anterior end is a smaller foramen for the nasalis externus of the profundus, where it passes to the external nasal glands.

The chondrification of the anterior parts of the capsule has outlined a large gap upon the dorsal surface, bounded by the columna ethmoidalis, lamina externa and anterior tectale, resembling in shape the large dorsal gap in Amblystoma. The floor of the capsule is represented by the cornu trabeculae and the antorbital process; the latter has not united to any more anterior capsular part, so that a foramen orbito-nasalis does not exist, nor does Wilder describe one in the adult.

The nasal capsule of Amphiuma differs considerably from that of any urodele thus far described. The large vacuities in the dorsal, lateral and ventral surfaces and the consequent lack of skeletal protection of the nasal epithelium is much in contrast to either Salamandra or Amblystoma and may represent either a reduction in parts or a permanent larval condition. So far as I know, a circumnarial ring does not exist in any other Urodele, the anterior part of the capsule being vaulted in all others, with the exception of the Caecilians and Necturus. The fusion of the planum basale with the cornua trabeculorum to form the hexagonal plate, is not common for other capsules, where in the older stages these parts are considerably removed from each other.

The narrow planum verticale develops dorsally from the median line of the planum basale, somewhat as in Cryptobranchus, and then unites laterally to the ethmoidal column which, as in Spelerpes, probably developed anteriorly from the cephalic margin of the trabecular crest. In no other capsule, thus far described, with the exception of Necturus, is there a complete absence of the lamina medialis. Anterior to the verticale the nasal organs are separated by membrane only, a wide gap extending from the medial margin of the cornu to the anterior tectale.

Amphiuma appears to be far removed from other Urodeles. It cannot be regarded as ancestral, as it is difficult to homologize the capsule of this animal, even in the early larval stages, with that of other genera; but it probably is reduced from more typical conditions more closely related to either Spelerpes or Cryptobranchus. In the origin of the verticale and in the form of the cornu which unites to the anterior extension of the externa,

Amphiuma resembles Cryptobranchus; and furthermore, the expansion of the ethmoidal column, at its middle to form the lateral parts of the capsule is alike in both. On the other hand, Amphiuma resembles Spelerpes in the size of the planum basale and the inter-nasal space, as well as in the posterior development of the ethmoidal column, evidence being lacking on this point in Cryptobranchus.

THE NASAL CAPSULE OF THE GYMNOPHIONA

EPICRIUM GLUTINOSUM

Considerable diversity of opinion has existed in the past in regard to the systematic position of the Caecilians. Cope (1889) classed them as a family of the Urodeles, related to them through Amphiuma; while the cousins Sarasin (1890), following Cope, also regarded them as Urodeles, considering Amphiuma a neotenic Caecilian. Kingsley (1902) reviewed the evidence as to the position of the group, showing that many points supposed to indicate relationships, were based upon erroneous statements or misconceptions and that the Gymnophiona are to be regarded as a distinct group, without any close relations to any other existing Amphibia.

To determine to what extent, if any, the nasal capsules of this group would shed light upon their relationships to the Urodeles, two larvae of Epicrium glutinosum were studied, in which chondrification was well advanced and the nasal capsules completely formed.

Peter (1898) has described the chondrocranium of a young Caecilian; and Winslow (1898) a stage in which the embryo is still spirally coiled within the egg, considerably younger than my earlier material. In contrast to all other Amphibia, the trabeculae of each side are double (Fig. 32), consisting of a dorsal and ventral bar in the position of trabecular crest and trabecula, the dorsal doubtless being the homologue of what Sewertzoff (1897) has called the alisphenoid cartilage of the Elasmobranchs. On either side of the eye, the dorsal and ventral trabeculae are united by a postorbital and preorbital band, the optic nerve passing through the large gap between them. Anterior to the preorbital band, the lower or true trabecula inclines toward the median line, and is united with its mate by a slightly convex planum basale (*pb*), which lacks the trabecular thickenings of the plana of Urodeles. The posterior and lateral margins of the planum are straight, the latter more anteriorly curving outward where it passes into the posterior margin of the cornu trabeculae, which forms the floor of the capsule; while anterior to the cornu the planum narrows considerably and is continuous in front into a pair of small processes, the tips of the trabeculae, separated from each other by a wide internasal space.

The planum verticale (*pv*) is a narrow plate of cartilage, arising from the anterior half of the median line of the basale and extending dorsally

to the upper margin of the nasal organs, completely separating them in this region from each other. The dorsal part of the verticale extends backward a short distance over the planum basale; while anteriorly it extends forward over the internasal space where it divides into three parts, a short median rostrum continuous with the verticale, and a pair of alary processes which extend ventrally and laterally, terminating near the tips of the trabeculae. In a later stage these alary processes develop anteriorly and laterally to form the vault of the capsule.

Anterior to the preorbital band, a wide band of cartilage, the lamina externa, forms the side wall of the capsule. It is pierced by two foramina, the smaller more posterior one for a small branch of the fifth nerve, while the profundus passes through the larger, more anterior one. Winslow (1898), in his early stage, describes a small antorbital process which extends outwards and forwards from the anterior margin of the preorbital band, much as in the Urodeles. In this stage, the anterior part of this process has united to the lateral parts of the capsule, enclosing the foramen above described, which must be the orbito-nasalis of Urodeles; so that it would seem that the lamina externa is formed of elements of an ethmoidal column and an antorbital process, although complete evidence as to the former is lacking.

Anterior to the foramen orbito-nasalis, the lamina externa widens slightly, its dorsal margin extending more medially, reaches to the level of the upper surface of the verticale, where a short process extends forward, separated from the remaining externa by a deep notch through which the superficialis passes to the nasal organ. Ventral to this notch and in the same horizontal line with the foramen orbito-nasalis, is another foramen through which a branch of the profundus nerve passes from the capsule.

Beyond this latter foramen, the lamina externa, more narrow than before, extends forward a short distance, ending in a blunt process in line with the anterior margin of the planum basale; while ventral to the foramen it is united to the cornu trabeculae, which supports the anterior end of the nasal sac, forming the only floor of the capsule, and enclosing the large ventral choanal gap.

Winslow has described a small cartilage bar, lying near the trabecula, just beneath the preorbital band, which is unassociated with any other part of the capsule. This he calls a palatine cartilage. In my material, this small bar is directly in line with the anterior part of the pterygoid process from which it is but slightly removed; and it would seem as though it was a part of the pterygoid which may have chondrified independently, or have separated from the more basal part of this process. Peter (p. 582, 1898) in his description of the pterygoid of Ichthyophis says: "Dagen findet sich in seiner Verlängerung parallel der unteren Trabekelspange ein

Knorpelstab, der sich bis in die Mitte des Opticusfensters erstreckt und seinerseits wieder in zwei Theile gespalten sein kann. Eine dichte Zellanhäufung verbindet die einzelnen Stücke mit einander und mit dem Fortsatze des Quadratum, so dass die betreffenden Elemente wohl als eines Ursprungs aufgefasst werden können." The term palâtal cartilage is a misnomer at least, for it is evident that the palatine bone, which is membrane in origin, could hardly be derived from this cartilage

The capsule of the older larva, 90 mm. long, (Fig. 33) differs considerably from that just described; the greatest change taking place in the more anterior parts. The ossification of many of the covering bones, and the resorption of certain cartilage structures, as well as the chondrification of others, has resulted in a capsule very different from that of any other Amphibian.

The preorbital and postorbital bands are much as before and need no further description, with the exception of the statement that they are more oblique, from medial and dorsal to lateral and ventral, than before. Through resorption, all connection between the preorbital band and the planum basale has been lost, so that a short caudal process from the planum on each side of the median line is a remnant of a trabecula, all intermediate parts having become ossified. The planum basale is shorter than before and the solum nasale or cornu trabeculae is now more posterior and in line with the caudal margin of the basale, which it unites to the lamina externa as in the early stage. The antero-lateral margin of the planum is more semicircularly excavate than before, and the tips of the trabeculae, extending beyond the basale are more slender, the internasal space between them being wider and deeper.

The planum verticale (*pv*), arising from the median line of the basale is wider than before, although not relatively as high. It is continued posteriorly into an elongate cylindrical process which extends backward to the level of the posterior margin of the basale, the dorsal root of the olfactory nerve lying lateral to it; while anteriorly it extends forward into a similar process reaching nearly to the tip of the snout. The alary processes, flanking the median rostrum of the verticale, which were just beginning to chondrify in the earlier stage, have now grown forwards and outwards covering the more anterior parts of the nasal sac and uniting with two lateral processes yet to be described, each forms a partial cupola, incomplete ventrally which protects the anterior ends of the olfactory sac. There is a small foramen near the lower margin of this cupola, through which a branch of the profundus nerve leaves the capsule.

The lateral wall of the capsule of this older stage is considerably different from that described above. The orbito-nasal foramen, the medial process of the lamina externa and their nerve relations are as before; but ventral to the foramen for the externus branch of the profundus, the

lamina externa bears a short posterior process from its ventral margin, a remnant of resorption now going on, so that the choanal gap in this stage is incomplete.

Just in front of the connection of the lower margin of the lamina externa to the cornu trabeculae, the lamina continues forward as two cartilage bars, the upper more cylindrical, the lower somewhat flattened, between which the organ of Jacobson is included. By the fusion of these parallel rods with the alary process above described, an elongate naris is formed which extends over one-half the entire length of the capsule; and at the same time these cartilages all unite to form the tip of the capsule, a flattened plate which covers the end of the nasal sac (Figs. 67, 68).

The nasal capsule of Epicrium is considerably different from that of any other Amphibian and can hardly be said to be Urodelan. In a very few points, resemblances can be drawn between the Caecilian and Urodelan structures; but these are so few, and the modification of the parts in the Caecilian is so great, that few close relationships can be established. The independence of alisphenoid cartilage and trabecula in Epicrium, find no parallel among the Urodela where these parts are continuous and form the wall of the cavum cranii; while in no other capsule do we find the deep and narrow external naris, as is present in my older stage.

The floor of the capsule is formed by a cartilage called by Peter (1898) the solum nasale, which can be none other than a modified cornu trabeculae which has developed laterally and has united to the lamina externa, just anterior to its fusion with the antorbital process. So that in this relation of cornu trabeculae, lamina externa and processus antorbitalis, there is a condition quite similar to the other capsules, such as Triton and Amblystoma, although superficial resemblances are lost. That the solum nasale was a cornu could not be derived from a study of the later stage where the greater development has taken place anteriorly, placing the solum in line with the planum basale; but the resemblance between the cornu trabeculae of my two weeks Cryptobranchus larva and this structure in my younger Epicrium seems to indicate the identity of these parts.

Superficially, the capsule of Epicrium resembles that of Amphiuma more than any other Urodele. In both the sensory parts are but poorly protected, wide gaps occurring in all sides of the skeleton. The presence of a six-sided planum basale, with its anterior prolongations, the planum verticale with its antero-lateral alary processes are structural resemblances between these animals. On the other hand Epicrium lacks the circumnarial ring of Amphiuma, and in its place has developed a partial cupola, possibly in correlation with the burrowing habit of this Amphibian.

In the origin of the planum verticale from the basale, as well as in the similarity of their cornua, Epicrium recalls Cryptobranchus; and it does not violate probability to assume that the small process developed

from the medial margin of the lamina externa is a remnant of an ancestral ethmoidal column, which originally was united to the more medial parts of the capsule.

Although some homologies may be drawn between the capsules of Epicrium and the Urodeles, the divergence between the two is sufficient to warrant the separation of the Caecilians and the maintenance of the Gymnophiona, distinct from all other Amphibia. Although the greater resemblance among the Urodeles is to Amphiuma, yet it is not sufficient to warrant the position of either Cope or Sarasin in the relationship of these groups.

COMPARISON OF THE NASAL CAPSULES IN THE URODELA AND GYMNOPHIONA

The nasal capsules of several families of Urodeles afford a basis for the division of this order of Amphibia into four groups, founded upon similarity of larval structures and the method of chondrification. In some forms, where larval characters were not at hand, adult characters were employed in the classification; in others the early process of development was the only criterion available. Of these groups, Spelerpes, Plethodon and Amblystoma form one; Salamandra, Triton and Diemictylus another; Amphiuma, although remote from Cryptobranchus in the later stages, is included with it in the third; while Necturus remains alone in the fourth group.

To recognize in the nasal capsules of the Urodela a complete phylogenetic development or gradual transition from one animal to another is impossible, for many gaps exist, concerning which evidences of structural relationships are wanting. On the other hand many resemblances in the development of certain structures in the nasal capsule may throw some light upon the inter-relationships of this Amphibian order.

Of the Urodeles included in this study, it would seem as if the capsule of the American species of Cryptobranchus possesses characters most ancestral and which show relationships to both Urodela and Anura. Regarding Cryptobranchus, then, as more primitive, Spelerpes, Plethodon and Amblystoma appear in an ascending series from the primitive condition; while Salamandra, Triton and Diemictylus are separated from them, but possibly related to them through some form like Spelerpes. Necturus may be regarded as a neotenic condition of Spelerpes, while Amphiuma is possibly reduced from the more primitive Cryptobranchus.

The two weeks larva of Cryptobranchus has a well-developed trabecular crest which is not present in corresponding stages of Spelerpes or Amblystoma; in the latter of which the development of the crest is apparently correlated with the chondrification of the ethmoidal column. Thus it would appear that in Cryptobranchus the dorsal crest is developed before the column, while in Amblystoma the reverse is true. In this respect, Spelerpes is intermediate between Cryptobranchus and Amblystoma, although more like the former; for in the only available stage of the older larva of Spelerpes, the crista is well developed, while the columna ethmoidalis is but partly chondrified. My material does not show the origin

of the ethmoidal column in Cryptobranchus, for in the five weeks larva it already unites the medial margin of the cornu to the crista; but judging from its relation to the capsule, and in its complete separation from its mate, these structures resemble those of Spelerpes in which the anterior part of the columna arises from the medial margin of the cornu and grows posteriorly along the nasal sac. Further, the anterior prolongation of the dorsal crista in Spelerpes, interpreted as the posterior part of a developing column, may also exist in Cryptobranchus, although conclusive evidence on this point is lacking.

In the 25 mm. Salamandra larva, the anterior end of the column is connected to the cornu trabeculae much as in Cryptobranchus; and yet the expansion from its posterior end, forming a small tectale prior to any connection with the crista, suggests an independence of the ethmoidal column, like that of Amblystoma. Although the dorsal crests of Salamandra develop along with the columna ethmoidalis, the two do not unite until a later stage, thus the posterior part of a developing column is lost in all Urodeles above Spelerpes. In Amblystoma, on the other hand, the ethmoidal column and the cornu trabeculae are chondrified independently of each other. In a 13 mm. larva, I have described a few cartilage cells above the medial margin of the cornu of the left trabecula only. This is the first appearance of an ethmoidal column which subsequently grows posteriorly along the median dorsal margin of the nasal sac. The fact that I observed these cells as chondrifying, at first, upon one side only, has no especial significance; but in the independent chondrification and the complete development of the ethmoidal column from in front backwards, prior to any association with the trabecula, Amblystoma differs from any other Urodele, except Necturus in which the independently chondrified ethmoidal column never unites to other parts of the capsule. Thus in the 20 mm. stage of Amblystoma, completely developed columnae ethmoidales parallel the trabeculae from their anterior tips to the choana; but do not unite to any crista, which here is greatly retarded in its appearance, not developing until the 25 mm. stage is reached.

The ethmoidal column in Amphiuma is more like that of Cryptobranchus and Spelerpes in the development of the posterior parts; there being no evidence of an anterior part of a column in the youngest larva studied. Somewhat as in Spelerpes, the anterior portion of the crista continues forward into a cylindrical bar along the medial margin of the nasal sac, and from its relation to other parts, as well as its position, it must be regarded as a columna ethmoidalis. As in Cryptobranchus, it gives off laterally a small process which may be homologized with the tectale, which then turns anteriorly, forming the lateral wall of the capsule, the lamina externa.

In all Urodeles studied, the planum basale is formed by a fusion of the trabeculae in the middle line of the skull; and in some forms, this plate,

which usually supports the anterior end of the telencephalon, is the only connection between the two capsules. In Cryptobranchus, Amphiuma, and Necturus, the planum basale of the larval stages is slightly convex, due to the origin of the verticale from its median line; while on the other hand the planum basale of Salamandra and Amblystoma are broadly concave, being in no way associated with the development of the verticale. The size of the basale is variable in the different groups; being very small in Cryptobranchus, Spelerpes and the larval Amphiuma, it increases in Plethodon and Salamandra, and reaches its greatest development in the larvae of Amblystoma where the fused basale and verticale form a thick anterior wall to the cavum cranii. Individuals approaching the end of metamorphosis show a reduction in the size of the planum basale, and in the adult stage it is greatly reduced, correlated with the development of other parts of the capsule and the increase in size of the sensory parts. In both larvae and adults of Triton and Diemictylus the planum basale is very small, and in the latter, is the only connection between the two capsules.

The planum verticale arises in different ways throughout the order. In Cryptobranchus, it arises from the median line of the basale as a small ridge, and later, uniting to the median margins of the ethmoidal columns, it forms a complete wall separating the internasal space from the cavity of the forebrain. The same is true in Amphiuma, although evidence is lacking as to the origin of the verticale, yet the later stages would suggest its development from the planum basale as in Cryptobranchus. The early larvae of Necturus have a small median ridge on the basale, probably a vestigial verticale; but it never develops and is less prominent in the later stage, a further evidence of the neotenic condition of this genus.

In the remaining groups, the verticale does not arise from the basal plate, but is developed by medial growths from the columnae ethmoidales which subsequently unite to the basale, so that the results are identical. In my material of Spelerpes, evidence of the formation of the verticale is lacking; but judging from the relation of the early columna to the cornu, and by the flat dorsal surface of the basale, it would appear that here, as in Amblystoma, the verticale arises from the medial growths of the ethmoidal columns. In a 25 mm. Salamandra larva, there is no evidence of a median verticale plate. The cornua and columnae are united just anterior to the planum basale, but internasal space and cavum cranii are continuous with each other. In the later stage, medial growths from the anterior parts of the columnae unite just above the anterior margin of the basale, and form a pons ethmoidalis, separated from the ventral plate by a circular gap, the fenestra ethmoidalis. This gap is only temporary in Salamandra, for by the more ventral chondrification of the pons, a complete verticale is formed and the internasal space and cavum cranii are completely cut off from each

other. In Amblystoma, this process is changed slightly, due to the independence of the ethmoidal columns from the cornua. In the 25 mm. larva, by medial growths of the columnae a pons has formed, so that in this stage the capsule is divided into dorsal and ventral halves, the only connection being the crista. By further chondrification of the region between the pons and the planum basale, a verticale is formed, the process continuing posteriorly, developing the solid thick cartilage of the 45 mm. larva.

A planum verticale does not chondrify in Triton and Diemictylus, so that internasal space and cavity of the forebrain are separated by membranous structures only. The pons ethmoidalis develops in Triton, uniting the dorsal medial margins of the capsules somewhat anterior to the planum basale, but it is completely lost in Diemictylus. Evidence is lacking as to the origin of the pons in Triton, but Born (1876) describes the process as a continuous growth of cartilage from the trabeculae, and not as independent parts; it would appear, then, that the pons has probably arisen by growths from the medial surfaces of the capsules, similar to that of Salamandra. In the absence of a pons, Diemictylus appears to be reduced from some form like Triton; the nasal capsule of these two being very similar in other details.

The antorbital process is present in all Urodeles, arising in all, except Cryptobranchus, from the ventral margin of the trabecula just back of the choana. It is directed laterally and anteriorly and in most Urodeles unites to the lamina externa, or to the cornu trabeculae, outlining the foramen orbito-nasalis, through which the nerves of the nasal region enter the capsule. In Necturus and Amphiuma, on the other hand, this process never unites to the more anterior parts of the capsule, so that a foramen is never formed, nor is there any posterior wall to the capsule as in those Urodeles where the antorbital unites to the tectale, as in Plethodon and Amblystoma.

Gaupp (1893) held that the antorbital process of Urodeles is homologous with the pterygo-quadrate arch of the Anura; and the terms palatine cartilage or ethmo-palatine have been indiscriminately used when referring to this structure. If we regard Cryptobranchus as ancestral, or at least more primitive, a conclusion I believe both the nasal capsule and the olfactory organs justify, then the relations and the development of the antorbital process in this animal may throw some light upon the homology of these structures. In the two weeks larva, in which the trabecular crests are already well-developed, there is no evidence of an antorbital process; but slightly posterior to its probable position, procartilage cells lie near the lateral ventral margin of the trabecula, which continue posteriorly into the pterygoid process of the quadrate. In the later stage, these cells have chondrified and, uniting to the pterygoid, have reached

forward, and, bending at right angles the bar has joined to the ventral margin of the trabecula in the region where the antorbital process occurs in all Urodeles. In the five weeks larva, there is no extension forward of this bar beyond its connection with the trabecula; but in the older larvae, a small process extends forward toward the capsule, an apparent continuation of the pterygoid; so that an antorbital process is formed which resembles in detail those of most other Urodeles. Because of the lack of older stages, I have no evidence as to the connection of the antorbital to the capsule, nor can I say just when the resorptive processes take place which establish the adult condition of the complete separation of the pterygoid from the capsular region.

Regarding Cryptobranchus as primitive, then it would appear that the Urodelan antorbital process is in reality composed of the anterior end of a pterygoid plus an anterior extension which secondarily becomes associated with the nasal region. In the Anura, both larva and adult, the pterygoid unites with the anterior part of the trabecula, as in the larval Cryptobranchus, suggesting here a common ancestry; and this relationship tends to support the original conclusion of Gaupp that the antorbital process of Urodeles, at least in its basal part, and the "palatine cartilage" of the Anura are homologous structures. The anterior part of the antorbital, however, is something else and may not be a part of the original pterygoquadrate arch; accordingly it would seem that in those Urodeles in which the pterygoidal condition is lost, that the entire structure had best retain the name antorbital process.

Winslow (1898) has described, in his second stage of Ichthyophis, an isolated cartilage in front of the anterior end of the pterygoid, which he calls the "palatine cartilage"; and interprets it as being a part of an original "palato-pterygoid-quadrate" arch. This cartilage can hardly be called a palatine, and the triple term applied to the pterygo- quadrate is a misnomer for the palatine bone is not cartilaginous in origin. It would appear, however, as though this small cartilage is a part of the pterygoid which at one time was connected to the antorbital process, and to the more proximal pterygoid. In his earlier stage, Winslow describes a small antorbital process which arises much as in the Urodeles from the trabecula. In my material, this process has united to the more anterior parts of the capsule outlining the foramen orbito-nasalis; and from its relation to the isolated part of the pterygoid we are safe in assuming that these parts were at one time in continuity, and in that sense the Caecilians are related to the common ancestor, from which Cryptobranchus on the one hand, and the Anura on the other, have arisen.

In the Siberian genus, Ranodon, Wiedersheim (1877, Fig. 69) has figured the relation of the antorbital process to the pterygoid much as it occurs in Cryptobranchus; which fact suggests that these genera may be

related, both having retained these ancestral characters. An older larva of Spelerpes, also figured by Wiedersheim (Fig. 108), has a caudal extension of the antorbital process, which he calls the maxillary cartilage, whose relation to the pterygoid suggests an earlier relation between the two.

In several of the Urodeles, as shown by figures of Parker (1876), and Wiedersheim (1877), a strong pterygoid reaches well forward from the quadrate, absent in some of my larvae but present in the adult. In the earlier larva of Amphiuma, a pterygoid process has not developed; but in the later stage it has chondrified well forward, nearly to the base of the antorbital. In all Urodeles, both processus antorbitalis and pterygoid are developed, but the proximity of the two varies greatly throughout the order, and I would hesitate to base any statement of relationships upon the relative extent of development of these structures; but no where except in Cryptobranchus and Ranodon is there any connection between them.

The openness of the nasal capsule of Amphiuma, together with the somewhat specialized anterior part, renders it difficult of homology with the more typical Urodele, and suggests that it is far removed from any other Amphibian. However, in the early method of chondrification, and in the development of some of the parts, Amphiuma appears to be more closely allied to Cryptobranchus. In both, the cristae trabeculorum are formed early, as well as the planum verticale, the latter arising from the median line of the basale and later becoming associated with the columna ethmoidalis. Further relationship is evidenced in the origin of the tectale as a lateral growth from the columna, giving rise in Amphiuma to the elongate lamina externa, along the lateral surface of the nasal sac. Meagre as these relationships may seem, Amphiuma appears to be nearer Cryptobranchus than any other Urodele, the anterior parts of its capsule having become secondarily acquired.

Although Salamandra resembles Amblystoma in some ways, the many differences between their capsules, such as the size of the planum verticale, the persistence of the foramen ethmoidalis in the former, and the origin of the ethmoidal columns, justifies their separation. In the persistence of the caudal process of the planum basale in the 25 mm. Salamandra, there is a resemblance to Cryptobranchus; but in the origin of the columnae ethmoidales from the medial margins of the cornua, Salamandra is more like Spelerpes.

Triton and Diemictylus are far removed from the group just described, but are probably related to it through Salamandra. The complete development of a lamina medialis, with the deep internasal space, and the anterior position of the olfactory sac in respect to the forebrain, as well as the persistence throughout life of the fenestra ethmoidalis, are characters common to both Triton and Diemictylus. The complete loss of a pons ethmoidalis in Diemictylus converts the fenestra into a gap, only a mem-

branous partition separating the internasal space from the cavum cranii. It would follow then, that Diemictylus is probably reduced from some form like Triton, and both genera are related to Salamandra which has developed along a line parallel to Amblystoma; and it is through some Spelerpes-like larva, as far as the nasal capsules are concerned, that Salamandra, Triton and Diemictylus are related to the group including Plethodon and Amblystoma.

Necturus and Proteus have often been regarded as primitive and Cope (1889) included them in a group, Proteida, apart from the Urodeles, although ancestral to them. I have not examined Proteus, but upon the basis of the nasal capsule of Necturus, which cannot be regarded as ancestral, Cope's position can not be affirmed. Pinkus (1894) called attention to the similarity of the nasal capsules of Necturus and Protopterus, a similarity based wholly upon the fenestration of the capsules, and not upon structural resemblances. The parts of the capsule of Necturus may be homologized with those of other Urodeles, but many differences have arisen in the appearance of these parts, so that relationships are very remote. Many parts of the capsule chondrify independently, later uniting to each other; the ethmoidal column, however, never unites to the other parts of the capsule, but by lateral growths produces the fenestrated roof over the nasal sac. Necturus is greatly retarded in the development of its nasal structures. In a 25 mm. larva only trabeculae are present, there being no evidence of cornua or planum basale or columnae, as in corresponding ages of Amblystoma and Salamandra. The earlier larvae of Spelerpes, Desmognathus, and Necturus seem to resemble each other very closely in their cylindrical trabeculae, slight cornual expansions and absence of trabecular crests. In the later stages, however, further resemblance is lost, for Spelerpes has gained true Urodelan characters while Necturus still possesses larval relationships; a fact, which, together with the retarded process of chondrification, suggests for Necturus that it may be a persistent larva, as has often been suggested.

As stated above, Cope placed Proteus with Necturus in the Proteida, regarding them as primitive Amphibia, and related to the Stegocephala by the presence of an intercalary bone. Kingsbury (1905) rejects Cope's thesis, affirming the absence of an os intercalare in Necturus, and suggested that Cope had probably regarded the posterior process of the opisthotic as an intercalary; furthermore he regards the intercalary of the Stegocephala as a membrane bone.

Norris (1911) working on the cranial nerves of Necturus, concludes that it cannot be regarded as primitive. The distribution of the cranial nerves agrees in detail with that of the higher Urodeles, a condition which would not be expected in a primitive form. Kingsbury, like others, has regarded Necturus as a neotenic larva, and would place it near Spelerpes.

His conclusion is based largely upon the absence of certain cranial bones, such as the nasals, prefrontals and maxillaries, which are present in other Urodeles. Rudimentary nasal capsules exist in the larvae of both Spelerpes and Necturus, and in the former a completely developed capsule is not present until a relatively late period, correlated with its retarded metamorphosis, the individual often not transforming until two or three years after hatching. On the basis of the nasal capsule, I am inclined to regard Necturus as a permanent larva, possibly related to the other Urodeles through a Spelerpes-like ancestor. The retention of the larval characters of the trabeculae and of the planum basale can certainly not be regarded as ancestral, nor can degeneration alone explain the present structure of the capsule of Necturus.

The phylogenetic position of the Gymnophiona has occasioned much diversity of opinion. Huxley (1875) stated that there was not the slightest indication of any approximation to either the Anura or the Urodeles. On the other hand, Cope (1889) even placed the family Caecilidae among the Urodeles, and regarded them as degenerate and related to the main line through Amphiuma; while the Sarasin cousins (1890) took the position that Amphiuma was a neotenic condition of the Caecilian. Kingsley (1902) discussed the views of both Cope and the Sarasins and established the conclusion, now generally accepted, that the Gymnophiona are to be regarded as distinct from either Urodela or Anura and placed in a separate order.

The nasal capsule of Epicrium presents little of classificatory value, except that it presents only distant resemblances to the characteristic Urodelan capsule. In the presence of dorsal and ventral trabeculae, Epicrium differs from all other Urodeles where the alisphenoid and trabecula are continuous and form the lateral wall of the cavum cranii. In the earlier stage, which Winslow studied, the ventral trabeculae unite to form the planum basale, but there is no extension forward of the trabeculae into cornua as in Urodeles; although in my earlier stage, which is considerably later than that of Winslow, small processes occur at the anterior margin of the basale, the probable tips of the trabeculae. The solum nasale, however, or floor of the capsule which unites the lamina externa to the planum basale, is a modified cornu, which in the older stage especially, is greatly removed from the position of the cornu trabeculae in Urodeles. The antorbital process, a lateral growth from the trabecula in the early stage of Winslow, later unites to the other parts of the capsule, as in Urodeles, bounding the orbito-nasal foramen. That the antorbital was at one time related to the parts of the pterygoid just posterior to it, is suggested by a sharp protuberance on its ventral margin toward the small independent part of the pterygoid; so that it would appear as if the processus antorbitalis and pterygoid cartilage of Epicrium were at one time united as in

Cryptobranchus, but the now intimate association of the former with the nasal capsule indicates that the Caecilian probably is far removed from ancestral conditions.

Epicrium is more like Amphiuma, of all Urodeles, although differing greatly from it. The greater similarity lies in the origin of the planum verticale from the median line of the basale and in the subsequent development of the alary processes which, in the later stages of both, partially cover the dorsal surface of the nasal sac. Further similarity lies in the modification of the cornu trabeculae which in both, forms the floor of the capsule, uniting the planum basale to the lower margin of the lamina externa, and partially supporting the nasal organ.

On the other hand, the parallel rods of cartilage which in Epicrium form the lateral wall of the capsule anterior to the solum nasale, uniting anteriorly with the alary process to form a partial vault, do not exist in Amphiuma, where the united elements of cornu and lamina externa expand into an oblique circumnarial ring. Further, the antorbital process of Amphiuma never unites to the capsule as in Epicrium, nor at any stage does a complete columna ethmoidalis exist in the latter form, so that there are many contrasts between the capsules of the two. Thus upon the evidence submitted by the nasal capsules, the position of Cope or Sarasin can not be supported, all conditions pointing to the complete separation of the Gymnophiona from the Anura or the Urodela.

THE NASAL CAPSULES OF THE ANURA

PIPA AMERICANA

The Surinam toad, a representative of the aglossate Anura, is unique among the Amphibia in its quiescent larval period, during which, the entire development takes place; so that the adult characters are formed before the animal takes up its free existence.

Parker (1876) has described the chondrocranium of a Pipa larva, considerably younger than my single stage, in which the complete fusion of the trabecular plates has obliterated the large hypophysial fenestra, so common to most amphibian skulls. In Parker's larva, the coalesced trabeculae form a broad, slightly emarginate internasal plate, which extends forward to the tip of the skull, where from each lateral margin a slender process bends posteriorly and, passing beneath the nasal organ, terminates in a rounded projection near the middle line of the capsule. Parker calls these processes the 'recurrent trabeculae', but it is easy to see that they are modified cornua, which in Pipa are more cylindrical than in most Urodeles, more like those in Cryptobranchus.

In my single stage, a Pipa larva two-thirds of an inch long, much of the cartilage of Parker's stage has been resorbed and the chondrocranium is more like that of other Amphibia. The broad intertrabecular floor is now reduced to a pair of trabeculae, which, with greatly reduced cristae, reach forward to the level of the eye, where they are united by a planum basale as in Urodeles (Figs. 34, 35, *pb*). This planum basale is broadly concave dorsally (Fig. 73, *pb*), and supports the olfactory lobes which lie above the posterior parts of the nasal organ; so that the olfactory nerve, which leaves the olfactory lobe from its ventral margin, passes through a large median foramen olfactorius (*fo*) in the basale, reaching the nasal sac at the choana. More anteriorly the planum basale narrows considerably, covering only the medial parts of the nasal sac and the nasal glands; at the same time expanding ventrally into a prominent keel, which separates the choanae of the two sides. Farther forward the planum basale is continuous with the planum verticale, which reaches forward to the tip of the skull, there to unite with other parts yet to be described thus completely separating the nasal organs of the two sides.

From each lateral angle of the planum basale, a small planum tectale (*pt*) passes obliquely outwards and forwards, covering the posterior part of Jacobson's organ where it empties into the nasal sac. At its lateral

posterior angle the tectale is continuous with the anterior portion of the pterygoid process, the two uniting to form a large triangular plate, Parker's ethmo-palatine cartilage, which continues forward into his pre-palatine spur; this process covering Jacobson's organ and part of the nasal sac. It is obvious that the terms ethmo-palatine and pre-palatal spur, used by Parker, are misleading for reasons stated before in this paper; and it would seem that the term planum tectale had best be used to designate this entire process. The extension forward of the pterygoid is the normal condition in the Anura, but among the Urodeles it is known to exist only in Cryptobranchus and Ranodon, this ancestral character having been lost in other Amphibia.

On the lower outer surface of the trabecula, at its junction with the capsular parts, is the foramen for the nasalis nerve, hence this is the orbitonasalis of the Urodeles. It follows from this identification, that the bar ventral to this is the greatly reduced antorbital while the roof of the foramen is as plainly tectale. The main part of the nerve courses forward through the cartilage, and the anterior end of the foramen lies on the ventral side of the tectale (Fig. 35). Another branch of this nerve emerges on the dorsal surface of the trabecula, turns medially and then ventrally and passes through another foramen to the medial side of the nasal sac parallel with the olfactorius. Just medial to this last foramen is the olfactory foramen for the I nerve which passes downward to reach the olfactory organ. From this it follows that the cartilage region anterior (and morphologically dorsal) to these nerves and their foramina must be the columna ethmoidalis.

At about its middle, the lower margin of the planum tectale gives rise to a short bar, at first extending ventrally and then medially and a little posteriorly, just above the anterior end of the organ of Jacobson. From near its base this bar gives rise to a cylindrical rod, which runs obliquely forward and inward to become continuous with the lower lateral surface of the planum verticale near its anterior end. In this course it passes, first, on the outer surface of the connection of the organ of Jacobson with the olfactory sac, then along the ventral lateral margin of the sac itself. The medial end of the ventral bar is connected with a second cylindrical cartilage, passing obliquely forward and inward to join the dorsal lateral side of the verticale at its tip, medial to the naris. Where the more ventral of these two cylindrical bars unites to the verticale, it expands into an alinasal cartilage, which supports the anterior part of the nasal organ, and is separated at its anterior end from the distal margin of the verticale by a crescentic groove, the external naris (Fig. 74).

The two cylindrical cartilages just described, have been known in the literature as the dorsal and ventral bars or processes, terms that convey nothing as to their homologies. From a study of Parker's early larva, it is

evident that the planum verticale is a reduced internasal plate, and that the so-called ventral process is a modified cornu. In the early stage, according to Parker, this cornu trabeculae is free from the tectale, ending near its median margin in a blunt process; but in the stage that I have studied the two are united, thus recalling the relation of these parts in the Urodeles. The dorsal process is evidently something additional in Pipa and cannot be compared to any Urodelan structure; although it exists in some form or other in all Anura, where it has been called the oblique cartilage because of its relation to the nasal organ. This cartilage may be a part of the original internasal plate of Parker's stage, the intermediate part between it and the verticale having been resorbed, leaving the elongate gap upon the dorsal surface of the capsule.

The capsule of Pipa is unlike any other Amphibian, differing markedly from any Urodele or Phaneroglossa, although similar in many ways to the other aglossal genus Dactylethra. The chondrocranium of Parker's younger larva is more complete and lacks the large gaps of the later stage, in which the resorptive processes have so greatly changed the appearance of the capsule. The planum tectale is evidently a growth from both the columna ethmoidalis and the trabecula, and has subsequently become united posteriorly to the pterygoid process, while anteriorly it has grown forward into the triangular process which has erroneously been called the ethmopalatine cartilage.

From the above identification of the ethmoidal column, it would appear that the planum verticale has developed by a fusion, in the middle line of the skull, of the trabeculae and the columnae ethmoidales; the ventral part of the verticale being trabecular in origin, the dorsal half derived from the united columnae ethmoidales. In this relationship, then, we have a condition very largely Amblystomal; for in the 34 mm. larva, the ethmoidal columns unite to the coalesced trabeculae to form the thick planum verticale so characteristic of Amblystoma, but which in Pipa is so greatly reduced in width.

BUFO AMERICANA

The nasal capsule of the Phaneroglossa is far more complex than that of the Aglossa, and the olfactory organs which lie entirely anterior to the forebrain are better protected by cartilage structures.

In a larva of *Bufo vulgaris*, one-third of an inch long (Parker, 1876), the trabeculae have fused to form an internasal plate, smaller than in Pipa, from which they diverge forward forming the cornua trabeculorum with an internasal space between them. So that this early stage of Bufo is similar to my 28 mm. *Rana viridescens*, yet to be described.

In my single stage of *Bufo americana*, whose body length is 9 mm., a complex nasal capsule has been chondrified; and resembles in many ways

the chondrocranium described by Gaupp (1893) of a 13 mm. *Rana fusca.* In this stage (Figs. 36, 37), a complete cavum cranii has been formed, bounded upon each side by the high alisphenoid cartilage, the internasal plate or planum basale forming the floor; while in front a perpendicular ethmoidal wall, pierced by a pair of olfactory foramina, separate the olfactory lobes from the nasal sac. Anterior to this ethmoidal wall, the planum basale (*pb*) forms the floor of the capsule; extending forward as a thick plate as far as the large naso-basales fenestrae, which open from the cavity of the capsule to the internasal space. The planum basale supports the medial parts of the nasal sac and its ventral diverticulum.

The planum tectale (*pt*) forms the roof of the capsule; reaching forward from the cavum cranii, somewhat more narrow and thinner than the basale, it covers the medial portions of the nasal sac to the external naris, in front of which it bends abruptly downward to form with the solum anterius, the anterior wall of the capsule. At its anterior end, the tectale expands laterally into a pair of alinasal cartilages, which curve outward and then upward, supporting the anterior end of the nasal sac and forming the ventral margin of the external naris; while from the base of these a pair of superior prenasal processes extend downward and somewhat medially into the internasal space (Fig. 82). Just medial to the external naris, the tectale is pierced by a small foramen on either side for the exit of the internus branch of the fifth nerve.

The planum verticale (*pv*) completely separates the nasal organs from each other. Arising from the median line of the perpendicular ethmoidal wall, it chondrifies anteriorly uniting the plana basale et tectale by their dorsal and ventral surfaces respectively. It extends forward to the tip of the skull, and its anterior margin separates the two large circular naso-basales fenestrae, which perforate the forward wall of the capsule (Fig. 80). These fenestrae surround the medial portion of the ventral nasal diverticulum together with the frontalis nerve, which passes to the intermaxillary gland in the internasal space.

In contrast to Pipa, a posterior wall is formed in the capsule of Bufo, by a lateral extension of the posterior part of the planum tectale, which curves outward and downward beyond the alisphenoid, uniting to the anterior prolongation of the pterygoid, which has already fused with the lower parts of the cranial wall. In the angle formed by the fusion of the pterygoid, tectale and alisphenoid, a small orbito-nasalis foramen conducts rami of the fifth nerve into the capsule; so that here, as in Pipa, there is a resemblance to the Urodeles, which furnishes a clue to the homologies of these parts (*fon*).

The united elements of lateral tectale and anterior pterygoid form a small rectangular cartilage which lies against the lateral surface of the nasal sac. This cartilage has been variously named the pars plana (Parker

1876) or planum terminale (Gaupp 1893); but from its relation to the tectale and the pterygoid, and from its position in respect to the nasal sac, the term lamina externa is best used here. Furthermore, it is apparently, at least in part, the homologue of the antorbital process of the Urodeles. Parker has also used the term prepalatine for this cartilage, which appeared to him to be in some way segmented from the more posterior parts; but I have no evidence that the lamina externa in Bufo is distinct from the other parts, for it appears to develop as a continuum, subsequently uniting to the more anterior parts of the capsule.

From the dorsal margin of the lamina externa, a narrow bar of cartilage passes upward, forward and medially over the lateral surface of the nasal sac to unite to the lateral margin of the planum tectale, slightly posterior to the external naris. This is clearly homologous with the dorsal process of Pipa, better known in both groups as the oblique cartilage (Fig. 81). The lacrimal duct, arising from the eye by two branches, passes forward over this oblique cartilage and down through a groove in the lamina externa to empty into a lateral diverticulum of the main nasal sac (Fig. 80).

Anterior to its connection with the oblique cartilage, the lamina externa continues forward into the lateral margin of the solum anterius, which forms the anterior wall of the cavum inferius, and is evidently developed from the cornu trabeculae, together with a dorsal extension of it. It is a thin plate of cartilage, bent upon itself, so that it includes in the angle the anterior part of the cavum inferius, which contains the more lateral parts of the ventral pouch of the nasal sac. More dorsally the solum anterius unites to the anterior margin of the planum tectale, its lateral margin expanding into the alinasal cartilage, already described. More posteriorly and within the capsule itself, is a short cylindrical bar of cartilage which extends from the lower margin of the alinasal cartilage to the anterior margin of the planum basale, thus separating the main nasal sac from the organ of Jacobson.

A small cylindrical inferior prenasal process, larger than the superior, extends forwards and slightly upwards into the intermaxillary glands. Below and behind, from the lateral angle of the solum anterius, a short process is directed posteriorly which rests beneath the diverticulum of the nasal sac, where it receives the lacrimal duct. This process may possibly be the tip of the cornu.

In contrast to Pipa, the capsule of Bufo much more adequately protects the olfactory organs; the gaps in its wall being smaller than in that genus. In Bufo the choanal fenestra is small and is distinctly bounded by cartilage, while in Pipa its boundaries are decidedly indefinite. Again Pipa has no circumscribed fenestra naso-basalis. Further differences between the capsules of the two genera are the greater depth of that of Bufo, correlated with a reduction in length, the result being an apparently more complicated condition of the anterior parts.

HYLA PICKERINGII

My work on Hyla has been restricted to a study of the adult, in which the development of membrane bones over the anterior end of the forebrain has been accompanied by a partial resorption of the posterior parts of the capsule, so that homologies are not always certain. Still Hyla in general has a somewhat close resemblance to its arciferan relative, Bufo.

Behind the planum verticale (*pv*), the planum basale (*pb*) has undergone resorbtion in the middle line, so that it is represented by a pair of narrow plates (Fig. 38). In front, however, the continuity of the two sides persists to the anterior end of the capsule, where the planum basale passes into the solum anterius. The perpendicular ethmoidal wall is lacking, as well as the posterior part of the planum tectale, so that the latter, posteriorly is reduced to an oblique bar on either side, the tectale being complete only in its anterior third, where it is expanded in front to twice its width. At the tip of the cranium, the tectale bends downward to pass into the vertical solum anterius.

All that remains of the planum verticale (*pv*) is a median septum, without a gap, uniting the anterior parts of plana basale et tectale. In front, where it joins the solum anterius, the tectale separates the two basal fenestrae, which are very much smaller than in Bufo. Dorsal and slightly lateral to these openings, is a small foramen for the exit of the nasalis internus nerve from the capsule.

The lamina externa (*le*), developed partly from the lateral part of the planum tectale, and partly from the anterior prolongation of the pterygoid process, forms the side wall of the capsule in the choanal region. Anterior to its connection with the tectale, this plate narrows considerably, and is interrupted by an oval gap, apparently a further evidence of resorbtion, as no sensory or nervous structures were found to pass through it. Just anterior to this opening the oblique cartilage (*oc*) passes upward and forward from the lamina externa over the nasal sac, to unite to the planum tectale at its widest part, its ventral side being expanded to form the posterior boundary of the naris (Fig. 77).

Just ventral to the origin of the oblique cartilage from the lamina externa, the lower margin of the latter expands outward into a small process which separates the cavum inferius from the more ventral cavum medium. More anteriorly, this part of the lamina externa unites with the lateral parts of the planum basale to form the solum anterius, which constitutes the anterior wall of both cavum inferius and c. medium, and the more medial parts of the capsule.

As in Bufo, the solum anterius is a thin plate of cartilage which curves upward and continues into the anterior margin of the planum tectale. Near its junction to the latter, a small alinasal cartilage extends laterally, forming the anterior boundary of the external naris; it is continuous med-

ially into a small superior prenasal process which extends ventrally and medially from the capsule. The inferior prenasal process is considerably longer than the superior; it arises from the planum basale just in front of the choanal gap and extends forwards and downwards into the internasal space (Fig. 78). Forming the floor of the c. medium, and extending backward beneath and slightly lateral to the lamina externa is a conical process considerably larger than that in Bufo; the possible remnant of the original cornu trabeculae.

Two small foramina pierce the solum anterius; the smaller and more dorsal conducts the nasalis internus from the capsule, while the larger more medial one is the fenestra naso-basalis, considerably smaller than that described for Bufo.

RANA VIRIDESCENS

The nasal capsules of the Arcifera and the Firmisternia are essentially alike, and, although I lack a series of stages showing the chondrification of the nasal capsule in Rana, the work of Gaupp (1893) has made it possible to compare the growth of the nasal capsule of the frog in connection with my own two stages.

In a larva 28 mm. long (entire length), in which the characteristic Anuran chondrocranium is beginning to develop, the nasal capsule (Fig. 40) consists of an elongate planum basale (*pb*), with the anterior extension of the trabeculae to the labial cartilages. The muscularis process of the quadrate (*mpq*) has fused with the lateral wall of the planum basale, and just above the junction of the two a dorsal process has arisen from the basale, which is to become the side wall of the capsule (Fig. 83). Gaupp (1893) has referred to this cartilage as the "Ethmoidal-pfeiler," but it differs from the ethmoidal column of Amblystoma in which chondrification of this bar is independent of the planum basale.

Medial processes from the dorsal margin of each columna ethmoidalis fuse in the middle line and form a pons (*pe*), recalling this same structure in Amblystoma and in Salamandra (Fig. 84). In all three genera the cavum cranii and the nasal cavity are continuous during a part of the larval development by means of the fenestra ethmoidalis (*fen eth*) ventral to the pons. Unlike Triton and Diemictylus however, chondrification from the pons to the planum basale soon develops the ethmoidal wall which separates these cavities.

Upon a level with the pons ethmoidalis, and arising from the dorsal part of the ethmoidal column, a small process extends laterally toward the muscularis process of the quadrate. A small opening, which must be regarded as the foramen orbito-nasalis for the nasalis internus nerve, pierces this process near its base; and from this identification, it follows that this process must contain parts of both planum tectale and processus antorbitalis, the latter being beneath the foramen. The more dorsal posi-

tion of the antorbital in this stage, may be explained by the presence of the muscularis process of the quadrate, and its attachment to the planum basale just ventral to the antorbital (Fig. 83).

Just in front of the choana, which opens into the mouth slightly anterior to the ethmoidal column, a longitudinal constriction of the nasal sac partially divides it into two chambers; one medial and dorsal, lying upon the lateral part of the trabecula, the other lateral and more ventral (it is the beginning of Jacobson's organ), which lies to the side of and to some extent beneath the trabecula.

The olfactory nerves of the two sides now pass from the forebrain forward and beneath the pons ethmoidalis to the nasal sac. Later, a chondrification ventral from the pons completely obliterates the fenestra ethmoidalis and, forming the ethmoidal wall, it outlines the two olfactory foramina in the anterior lateral angles of the cavum cranii.

Anterior to the planum basale, the trabeculae diverge, enclosing a wedge-shaped internasal space between them. At first more narrow, each trabecula widens nearer its tip; and, just in front of the level of the naris, bends abruptly downward to end near the inferior labial cartilage. This vertical portion of the trabecula is apparently what Gaupp calls the superior labial cartilage, and which he figures as a discrete element in both his earlier and later stages. I do not find in my material any line of demarcation between the trabeculae and the superior labial cartilages.

I have had no material intermediate between the larval stage just described and a young frog soon after metamorphosis. But it is easy to see, however, that the changes undergone are about as follows; this account agreeing substantially with that of Gaupp.

As in a larva of Bufo, a tadpole of Rana approaching the end of metamorphosis, according to Gaupp, shows a decided reduction in the sagittal plane of the anterior part of the nasal capsule. This reduction is caused by a partial resorption of the earlier larval trabeculae, so that the definite nasal capsule is formed by a development of the posterior parts of the trabeculae, together with certain independently chondrified parts.

Subsequent to the closure of the fenestra ethmoidalis, by the development of a perpendicular ethmoidal wall, the planum verticale chondrifies anteriorly, separating the nasal organs of the two sides and uniting the planum basale in its median line to the planum tectale, which has grown forward from the dorsal margin of the pons and the ethmoidal column. The lamina externa forms the side wall of the capsule, and develops from the lateral part of the tectale; it unites to the oblique cartilage, which chondrifies independently and lies diagonally across the nasal sac from the lamina externa to the more anterior tectale.

In the anterior part of the capsule, the greatest modification takes place. The loss of the labial cartilages and the anterior parts of the trabeculae

causes a shortening of the capsule, which is accompanied by an increase in its depth. In front, each trabecula gives rise to a solum anterius which forms the anterior wall of the capsule; and at its junction to the tectale each solum gives rise to an alinasal cartilage, which supports the anterior end of the nasal sac and forms the posterior boundary to the external naris. The large naso-basal fenestrae between the medial margins of the anterior walls of the capsule and the planum verticale open from the nasal cavity to the internasal space much as in Bufo.

In this stage, the articulation of the lower jaw has moved backward, so that the deeply curved muscularis process of the quadrate is more posterior; and, as a result, the pterygoid has united to the capsule at the point of origin of the tectale from the ethmoidal column, the anterior maxillary process reaching forward from the junction of the two.

In a young adult of *Rana viridescens* (Figs. 85, 86) there has been a relative reduction in the height of the verticale, although the proportion of breadth to length is approximately unchanged. Anterior to the cavum cranii, planum tectale, basale and verticale have fused into a thick plate, recalling the association of these same structures in Amblystoma. The olfactory foramen (*fo*) opens obliquely forward from the antero-lateral angle of the cavum cranii to the nasal cavity just beneath the foramen orbito-nasalis the posterior opening of which lies adjacent to the lateral margin of the cranial wall. Lateral to the foramen orbito-nasalis, the fused tectale and antorbital curve outward and downward over the choana and continue posteriorly into the pterygoid, while anteriorly a small maxillary process reaches forward midway to the tip of the capsule.

The nasal sac is completely covered dorsally by the lateral parts of the planum tectale which reaches forward to the tip of the cranium, and is considerably narrower at the anterior end. At about the middle of the tectale, an oblique cartilage bar (*oc*) extends backward and slightly outward, ending bluntly near the anterior end of the maxillary process (*amp*). Although unconnected in this stage, these two structures are probably the homologue of the lamina externa and the oblique cartilage of the larva.

The nasal sac opens to the exterior just anterior to the oblique cartilage, where the alinasal cartilage, continuous anteriorly into a superior prenasal, forms the floor of the naris. Beneath the alinasal, but connected to it, is a thick cartilage, the crista subnasalis (*cr s*) possibly a remnant of the earlier solum anterius, although evidence is lacking here. Anterior to the crista sub-nasalis is the inferior prenasal process, which extends ventrally from the capsule; while directly above it is the fenestra naso-basalis, greatly reduced here, and more like that in Hyla.

COMPARISON OF THE NASAL CAPSULES IN THE ANURA

The division of the Anura into the suborders Aglossa and Phaneroglossa is borne out by this study of the nasal capsules; for Pipa would appear to be far removed from the other Anura, and because of the large vacuities in the chondrocranium it may be said to be more like the Urodeles.

In all of the Anura, the extension of the pterygoid process to the nasal capsule is the normal condition, and recalls this relationship in Cryptobranchus Furthermore, the planum tectale, apparently a lateral growth from the. columna ethmoidalis, unites to the pterygoid, the two forming in Bufo the lamina externa, which forms the side wall of the capsule; while in the adult Rana, the anterior connection of the lamina externa is lost, the united pterygoid and tectale forming the anterior maxillary process.

The cavum cranii of Pipa is not as well developed as in other Anura, the alisphenoids being but little higher than the planum basale, and less crest-like in their appearance. The forebrain in Pipa lies dorsal to the posterior part of the nasal sac, rather than posterior to it as in Bufo; and, if the olfactory nerve may be regarded as sufficient evidence for the determination of homologies, then that part of the basale in Pipa, anterior to the foramen olfactorius, must be the perpendicular ethmoidal wall in Bufo and other Phaneroglossa. This change in the relative position of these parts may be explained by the statement of Gaupp that the chondrocrania of larvae of *Rana fusca* suffer a reduction in the sagittal plane during metamorphosis.

In both groups, the roof of the capsule, anterior to the region just described is formed by a fusion in the middle line of the ethmoidal columns, which also unite to the planum verticale. In Bufo, the extent of the tectale lateral to the verticale is considerably more than in Pipa, where the medial parts of each nasal sac are but slightly covered and suggest for Pipa a more complete fusion of the ethmoidal columns. There is no floor of the nasal capsule in Pipa, while in all the Phaneroglossa the planum basale extends forward from the cavum cranii to the tip of the capsule, where each lateral angle expands into the alinasal cartilage. The presence of these alinasals in Pipa would suggest that the ventral half of the planum verticale must be a fused and greatly reduced trabecular plate, homologous to the anterior planum basale in the Phaneroglossa.

The lateral wing of the capsule, the so-called ethmo-palatine of Parker or planum terminale of Gaupp, but more properly designated the lamina externa in Bufo, is formed, partly from the pterygoid and partly from the columna ethmoidalis. In both groups two cartilage bars unite the lamina

externa to other parts of the capsule; although differing in their relations to each other, and in their position in the capsule, their homology is very evident. The ventral of these two bars is the cornu trabecula, more slender and cylindrical in Pipa; while in Bufo it is greatly reduced in length, considerably broader and has been designated in this paper as the solum anterius. The junction in both groups of this cartilage with the alinasal cartilage is a further evidence of their homology. The dorsal of the two bars, above mentioned, is apparently an additional structure in the Anura, for I do not recognize it in any Urodele. The term oblique cartilage seems to best designate this bar, extending, as it does, obliquely forwards and upwards from the lamina externa to the planum tectale, or as in Pipa to the tip of the planum verticale.

CONCLUSIONS BASED ON THIS STUDY

PHYLOGENY OF THE NASAL CAPSULE IN AMPHIBIA

The cartilaginous nasal capsule of Amphibia must have been derived from that of some lower vertebrate, be it Dipnoan or be it Crossopterygian, and that in turn from the Elasmobranch. So far as our knowledge goes, the Elasmobranch capsule is a continuous cartilaginous structure with no gaps or openings except that for the naris and the small foramina for the passage of nerves. The amphibian capsule, on the other hand, has interruptions in its walls; some of which are due to the fact that in the adult, bones appear in the nasal region and thus do away with the necessity of the persistence of protecting cartilages in certain places. Some are caused by the development of a complete olfactory duct with its choana, in addition to the naris.

Within the class of Amphibia there are many differences between the various capsules, caused by differences in the size and shape of the covering bones, by the changes in the development and shape of the organ of Jacobson, the modifications of the lacrimal duct, as well as by the difference in the size and shape of the olfactory sac. It follows, therefore, that in the history of the amphibian capsule, two stages should be recognized; one a progressive process in which the capsule is built up, a repetition of the ancestral (piscine) history, and the other in which this capsule is reduced and changed into the definitive form.

In following these two stages, we are hampered in our conclusions by the fact that we have no accurate and detailed account of the development of the capsule of any fish, and expecially in those groups universally recognized as ancestral. Neither Parker nor Sewertzow give any details of the development of the Elasmobranch capsule which can be used in this connection. The studies made in this laboratory of the development of the capsule in Acanthais only go far enough to show that it consists, when it first is recognizable, of a rudimentary floor, and an even more incomplete roof, and that these arise independently of the trabeculae or other cranial elements.

The foregoing studies show, that in those forms where the development has been followed with any detail from one stage to another, that there is first a progressive development, apparently tending toward the formation of a complete capsule like that of the adult Elasmobranch. Then alterations occur, largely degenerative in character, which result in the partial reduction of the floor and roof. These progressive changes

are well exemplified in Necturus where, even in the adult, the capsule is more nearly entire than in any other genus; a condition which may be explained on the supposition that Necturus is to be regarded, not as more primitive than other Urodelan genera, but as a permanent larva, a view which has been advocated by many in recent years.

In Amblystoma, as detailed in the foregoing pages, this history is carried farther. There is first a progressive development tending toward a complete capsule, but never approaching completeness as nearly as does the adult Necturus. Then, in conjunction with the process of metamorphosis, there comes a resorption of parts and a modification of those that persist, resulting in large vacuities in both floor and roof of the capsule. These steps are detailed above, and the final result is an envelope for the olfactory organ in which parts are recognizable as homologous with those of the capsules of the adult Anura.

In the history of the capsules in all Amphibia the following parts are concerned. The two trabeculae are united in the 'ethmoid' region by what Gaupp and others have called an internasal plate. This lies below the tip of the brain and is the 'ethmoid plate' of Winslow or the 'planum basale' of the foregoing description. In front of this planum basale, the trabeculae continue as the cornua trabeculorum to the tip of the skull, supporting the anterior part of the nasal organ. In several Urodeles, where I have studied the early larval stages (this history has not been followed in the Anura with sufficient detail to say whether it holds for them) a bar of cartilage, the columna ethmoidalis, arises on the upper medial side of the olfactory organ (either independently or as an outgrowth from the cornu) and lies parallel to the lower trabecula. By a lateral growth from this ethmoidal column, the planum tectale extends over the dorsal surface of the nasal sac, uniting in the later stages to the cornu trabeculae. The term lamina cribosa, used by Winslow (1898) and Terry (1906) to designate this cartilage is a misnomer, for it is hardly necessary to say that it cannot be homologous with the structure bearing the same name in the mammals, as it lies wholly dorsal to the olfactory nerve.

In the larvae of several Urodeles, and in my single larva of Rana, the ethmoidal columns of the two sides are connected by a pons ethmoidalis which roofs the fenestra ethmoidalis leading from the cavum cranii to the ethmoid region. This is only a temporary condition in most amphibia where the chondrification of the planum verticale closes the fenestra and unites the floor and roof of the capsule. In Triton and Diemictylus, on the other hand, the planum verticale never develops; so that cavum cranii and internasal space are separated by membranous structures only.

The last special element entering into the formation of the capsule is the antorbital process, which needs a somewhat longer discussion. In the Urodeles, a process arises from the side of the trabecula just back of

the choanal region; it extends laterally a short distance, then turns forward and later uniting to the planum tectale forms a part of the lateral wall and floor of the capsule. This has almost universally been called the antorbital process; but the larva of Cryptobranchus shows what it really is. In my second larva of this animal the pterygo-quadrate bar extends forward from the hinge of the lower jaw and joins the trabecula at the same point from which the antorbital projects in other Urodeles. In Ranodon judging from Wiedersheim's figure (1877, Fig. 69), there is a similar connection of the pterygoquadrate with the anterior part of the skull. Elsewhere in all described Urodeles, as far as I have been able to discover, there is only an extension of the pterygoid process forward from the quadrate towards the capsular region; and even in the adult Cryptobranchus (and this holds also for the Japanese species, as figured by Parker) the connection between the pterygoid and the structures farther forward is lost.

In all the Anura, on the other hand, the pterygoid cartilage is connected throughout life with the nasal capsules. In this respect Ranodon, and to a less degree Cryptobranchus, approach the Anura more closely than any of the other Urodeles. It is usual to regard this arch as the homologue of the upper jaw of the Elasmobranch, which, with the development of the osseous upper jaw of the Teleostomes and higher groups, has lost its original function as a part of the feeding apparatus, and has fused with the side of the cranium, its middle portion dropping out in the process. It may be remarked parenthetically, that the name palato-quadrate commonly given this arch is incorrect, as it contains no palatal element and no part of the palatine bone is developed from it.

In no Elasmobranch is there any extension of the pterygoid as a distinct process beyond the curve of the arch of the upper jaw. On the other hand, in all of the Amphibia there is such a forwardly directed process, the antorbital, already referred to. It would then apparently follow that the antorbital process of the Urodele, is in its basal part, the anterior end of the pterygoquadrate, while its anterior portion is a new formation. That this interpretation is correct, is supported by all of the Anura that I have studied.

In my earlier stages of Salamandra (in which there is no connection at any stage between the pterygoid process and the structures farther forward) the antorbital process is developed and extends forward beneath the nasal capsule; but as yet it is unconnected distally with any other cartilage. Just dorsal to the base of this process, both the ophthalmic and superficialis branches of the fifth nerve pass into the capsular region. Thus the antorbital process is ventral to these nerves. In the oldest larva that I have of this genus, the roof of the capsule (planum tectale) has extended back so that its posterior margin overlies the base of the antorbital, while between the tectale and the antorbital there is a very large gap.

In other genera, both Urodele and Anuran, these same nerves pass through a small foramen in the region corresponding to that in Salamandra; and since nerves and their distribution may be regarded as sufficient criteria, it follows that this part of the capsule is a composite of a ventral antorbital and a dorsal tectale.

In Pipa, Bufo and Rana, the pterygoid joins the side of the anterior part of the cranium, this distal portion being nearly at right angles with the axis of the skull. At the anterior side, a process extends forward from the bend in the pterygoid, forming the postero-lateral wall of the capsule. This is the lamina externa in Bufo and Hyla; and in the adult Rana, where its anterior connection with the capsule has been lost, the lamina externa becomes the anterior maxillary process. This anterior process, then, reaching forward from the pterygoid, be it ethmo-palatine (Parker 1881) or planum terminale (Gaupp, 1893) can be none other than the antorbital process of the Urodeles; and it is joined either in front (Bufo and Rana) or upon its ventral surface (Pipa) by two cartilages, the oblique cartilage bar and the cornu trabeculae, the latter being designated the solum anterius in the Phaneroglossa.

On the basis of the nasal capsule, Epicrium is far removed from either the Urodeles or the Anura; and it would appear that the grouping of the recent Amphibia into three orders by Müller (1832) is borne out by this study. Anterior parts of a pterygoid reach well forward into the nasal region, and although there is no continuity between the pterygoid and the antorbital (which in my material has united to the more anterior parts of the capsule); yet a sharp process extending from the latter toward the pterygoid leads to the assumption that at one time these parts were continuous and that the antorbital process in Epicrium has had a pterygoidal ancestry.

CLASSIFICATION OF THE AMPHIBIA

The earliest classification of the Amphibia did not include the extinct with recent forms, largely because of the uncertainty of the systematic position of the fossil forms, which were regarded by some as reptiles. It was not until 1854 that Vogt stated that Archeosaurus and all the Labyrinthodontia are amphibians and not reptiles. Owen (1866) was among the first to propose a classification to include both extinct and recent forms.

Since these earlier days most Zoologists divide the class into four orders: namely; the Anura, Urodela, Gymnophiona and Stegocephala. There have been few variations in the subdivisions in the Anura and the Gymnophiona, but with regard to the Urodeles ideas have differed greatly. Some would recognize only Salamandrina and Ichthyoidea; while more commonly the tendency has been to subdivide the group into Perenni-

branchs, Derotremes and Salamandroidia,[1] according as external gills persist through life, as gill clefts remain permanently open or, in the latter, as the animals undergo a complete metamorphosis, losing their external gills and gill-clefts.

Strauch (1870) divided the Urodeles into two sub-orders, the Salamandrida and the Ichthyoidea. The basis of his classification was the presence or the absence of eyelids, the arrangement of the palatal teeth, and the permanence of gills and gill clefts. The Salamandrida were subdivided into two groups according to the arrangement of the palatal teeth. Those Urodeles in which these teeth formed diverging rows upon the inner margin of the palatine were grouped as the Mecodonta; while the Lechriodonta included those animals in which the palatal teeth form converging rows along the posterior margin of the palatine. The Mecodonta embrace six genera of which Salamandra, Triton and Diemictylus are represented in this paper; while of the thirteen genera included in Strauch's Lechriodonta, I have studied Amblystoma, Plethodon and Spelerpes.

The Ichthyoidea are divided into two groups, the Cryptobranchiata and the Phanerobranchiata, according to the persistence of gill clefts only or of both gills and gill clefts. Cryptobranchus, Menopoma and Amphiuma belong to the former group; while Necturus, Proteus and Siren are included in the latter.

The nasal capsules would support a classification of the Urodeles similar to that of Strauch. In the fore-going pages, I have included Spelerpes, Plethodon and Amblystoma (part of the Lechriodonta of Strauch) in a group descended from the more primitive Cryptobranchus; while Salamandra, Triton and Diemictylus (the Mecodonta of Strauch) are included in a group connected with the other group through some form like Spelerpes. I have regarded Cryptobranchus as more primitive, and Amphiuma as closely related to it, although not in the main line of descent. Strauch has grouped Necturus and Proteus into the Phanerobranchiata more distantly related to Cryptobranchus, while I have regarded Necturus as a permanent larva of some Spelerpes-like animal. I have not studied Proteus, but have placed Necturus in a separate group in keeping with the later Perennibranchiate classification.

Accordingly on the basis of the nasal capsules, I would adhere to the classification of the Urodeles into three suborders, the Perennibranchiata [Phanerobranchiata (Strauch)], the Derotrema [Cryptobranchiata (Strauch)] and the Salamandroidia. The latter may be divided into two groups, and, following Strauch, the terms Mecodonta and Lechriodonta may be retained.

[1] In many text books, this is given as Salamandrina, but the group was called Salamandroidia by Fitzinger (1826) who in the same place describes a genus Salamandrina. Confusion is therefore avoided by restricting the latter name to the genus while Salamandroidia with its ordinal termination may be retained for the larger group.

Cope (1889) misled by a supposed ethmoid bone in Amphiuma placed the Caecilians with the Urodeles, in which view he was later supported by the Sarasins (1890). Kingsley (1902) definitely determined the position of the Caecilians and maintained Huxley's conclusion that the Gymnophiona have probably separated from the ancestral Amphibia back in the early Carboniferous period. The nasal capsule of Epicrium is further evidence of the wide divergence of this group from all other Amphibia.

The Anura are readily separated into two groups, on the basis of the nasal skeletons, and these agree with the extablished classification into the Aglossa and the Phaneroglossa. Cope's subdivision of the latter into Arcifera and Firmisternia is not so readily recognized in the nasal capsules of my material, although there are more resemblances between the capsules of Bufo and Hyla, than of either with that of Rana.

AMPHIBIAN ANCESTRY

The Amphibians appear, as Stegocephals, in the Carboniferous period, and although from the first they are considerably diversified, there is not known a single trace of any tetrapodous vertebrate in the Devonian with the sole exception of a single footprint from the Pennsylvanian. In the Devonian and somewhat earlier, fishes belonging both to the Dipnoi and to the Crossopterygian ganoids occur, and both of these piscine groups have been invoked by various zoologists as the ancestors of the Amphibia, possibly the tendency of the evidence at present favoring the Crossopterygians.

All of the amphibians of the Carboniferous, with the possible exception of Pelion, were caudate. Moodie (1916), the latest to study these ancient forms, is inclined to regard Micrerpeton, a small Salamandra-like form, as representing the ancestors of the modern groups, with Necturus as an annectant genus. He bases this conclusion upon the resemblances of the skull, the form of vertebrae and ribs, the peculiarities of the lateral line system, and the presence in both of 'ventral scutellations,' a view which closely resembles the earlier ideas of Cope.

But it would seem as if Moodie was leaning upon a weak reed in invoking ventral scutellations as an argument, no matter what view one may take with regard to the other points of resemblance. It is well known that many of the Stegocephals had ventral scutes, plates or bars upon the ventral surface of the body, but the universal view is, that these structures were purely dermal, belonging like scales of fishes to the skin. Moodie cites Wilder as stating that Necturus had small cartilages in the ventral region, and apparently he regards these as the homologue of the ventral armor of Stegocephals. But there are very important differences between the two.

Most students have regarded the gastralia of Sphenodon and the Crocodilia as derivatives from the plates and bars of the Stegocephals. These latter are also suggested as forming the elements from which the clavicles and episterna of the higher vertebrates are derived. In Sphenodon, according to Osawa (1896) and Howes and Swinnerton (1901), the gastralia develop without any cartilage basis, and, with the single exception of Schneider, no one has ascribed any cartilage stage for the gastralia of the alligators and crocodiles; while Voeltzkow and Döderlein (1901) shows that in Crocodiles there is no cartilage stage in these structures. In short, the great bulk of the evidence goes to show that these so-called abdominal ribs are dermal elements without any cartilage stage.

Wilder explicitly states that the cartilages he describes in the ventral surface of Necturus lie in the myocommata; that is, entirely deeper than the skin. He compares them to sternal elements. Hence it would appear that other evidence than these intermuscular cartilages must be brought forward to support his thesis.

According to Moodie, Micrerpeton has well developed nasals, prefrontals and elongate maxillaries, all of which are lacking in Necturus. Now if Necturus is to represent the ancestors of the modern Urodeles in which these same elements are present, we have the difficulty of explaining how these bones disappeared from the line of descent and then were reformed in the later generations.

Cope regarded Necturus as primitive because it possessed what he called an intercalary bone in the skull, an element which he also recognized in the Stegocephals. But Kingsbury (1905) says, that, at least in Necturus, Cope's intercalary was the caudal extension of the opisthotic.

Nothing is known of the cartilaginous nasal capsules of the Stegocephala, so that no comparison can be made between those of Necturus, and Micrerpeton. However, the complete isolation of the Necturan capsule and its wide separation from that of the other Urodeles, is certainly one argument against the ancestral position of this animal. Furthermore, the absence of maxillaries, nasals, and prefrontals in Necturus is one of the arguments of Kingsbury (1905) in regarding Necturus as a permanent larva, a conclusion which a study of the nasal capsule suggests.

Moodie (1916, p. 24) says: "The condition found in the skull of Cryptobranchus alleghaniensis will represent pretty accurately the condition of most of the coal measures Amphibia." Farther than this no emphasis is laid upon the primitive condition of Cryptobranchus. However, because of the simplicity of the nasal capsule, the persistence of the pterygoquadrate arch, and also because of the time and manner of the ossification of the skull, I am inclined to regard Cryptobranchus as more primitive.

As a study of the nasal capsules suggests, the Urodeles are widely separated from the Anura. Fossil Anura occur in an excellent state of

preservation as far back as the Tertiary. Earlier than this all known fossil forms are caudate, with the exception of a single specimen, Pelion lyelli, found in the Carboniferous, which closely resembles recent Salientia. Should Pelion prove to be a primitive Anuran, then the Urodeles and the Anura have probably separated from the Stegocephalan ancestor as far back as the late Devonian or early Carboniferous period.

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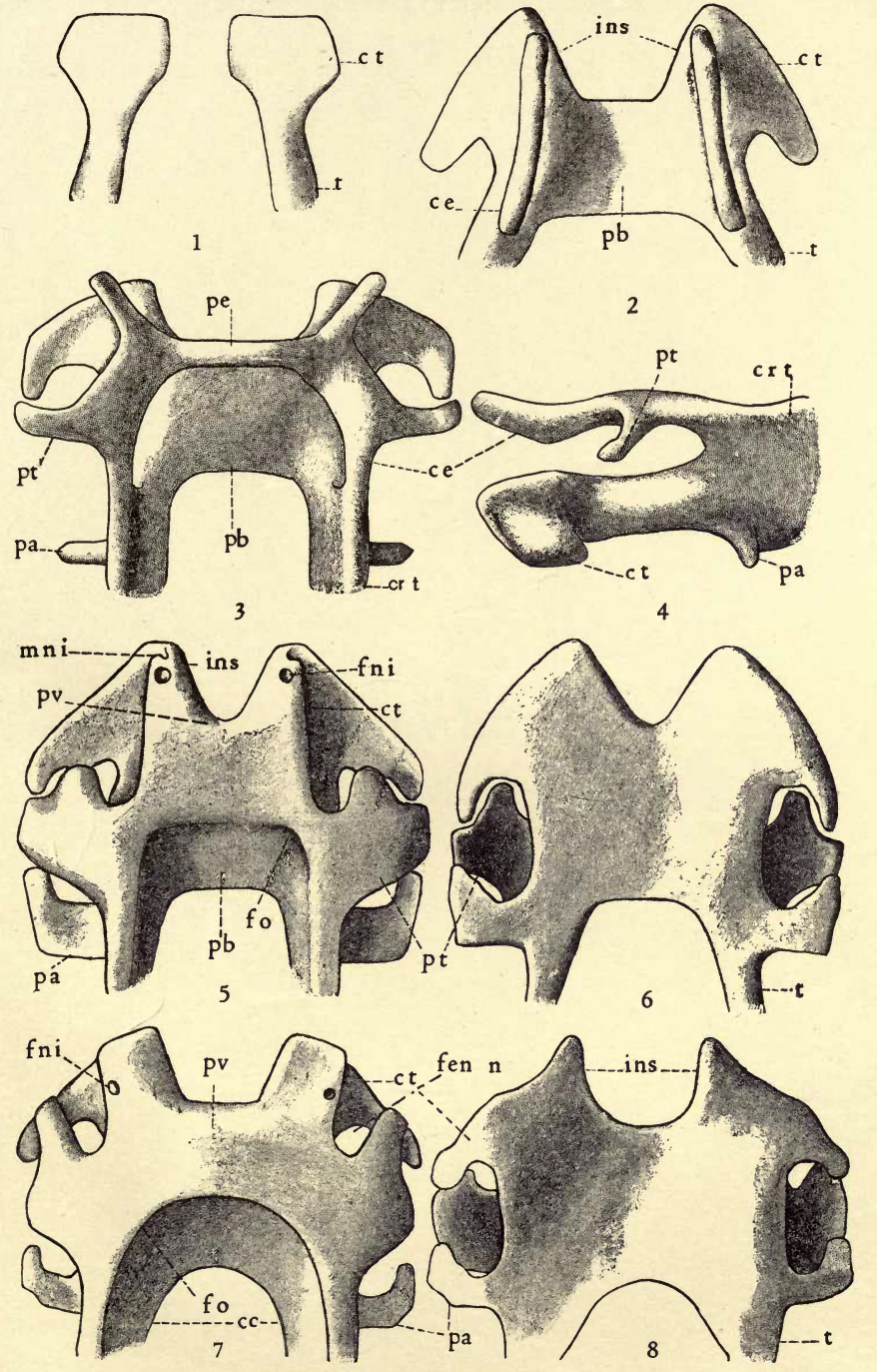
PLATE I

EXPLANATION OF PLATE

Fig. 1.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 11 mm. long.
Fig. 2.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 20 mm. long.
Fig. 3.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 25 mm. long.
Fig. 4.—Side view of model of nasal capsule of *Amblystoma punctatum* 25 mm. long.
Fig. 5.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 34 mm. long.
Fig. 6.—Ventral view of model of nasal capsule of *Amblystoma punctatum* 34 mm. long.
Fig. 7.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 45 mm. long.
Fig. 8.—Ventral view of model of nasal capsule of *Amblystoma punctatum* 45 mm. long.

ce	columna ethmoidalis	*mni*	median nasal incisure
cr t	crista trabeculae	*pa*	processus antorbitalis
ct	cornu trabeculae	*pb*	planum basale
fen n	fenestra narina	*pe*	pons ethmoidalis
fni	foramen nasalis internus	*pt*	planum tectale
fo	foramen olfactorius	*pv*	planum verticale
ins	internasal space	*t*	trabecula



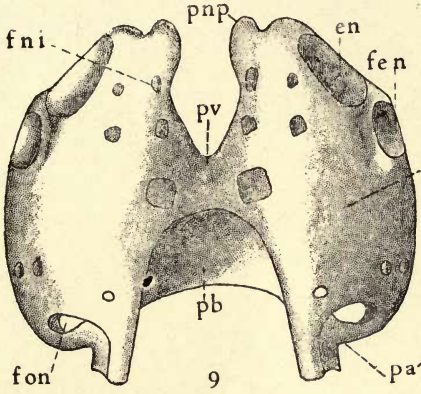
HIGGINS NASAL ORGAN IN AMPHIBIA PLATE I

PLATE II

EXPLANATION OF PLATE

Fig. 9.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* 55 mm. long.
Fig. 10.—Dorsal view of model of nasal capsule of *Amblystoma punctatum* at the end of metamorphosis.
Fig. 11.—Dorsal view of model of nasal capsule of *Salamandra maculata* 25 mm. long.
Fig. 12.—Dorsal view of model of nasal capsule of *Salamandra maculata* 38 mm. long.
Fig. 13.—Dorsal view of model of nasal capsule of *Salamandra maculata* at the end of metamorphosis.
Fig. 14.—Dorsal view of model of nasal capsule of *Diemictylus viridescens* 38 mm. long.

c	cupola	*fo*	foramen olfactorius
cc	cavum cranii	*fon*	foramen orbito-nasalis
ce	columna ethmoidalis	*ins*	internasal space
ce p	cephalic process	*le*	lamina externa
cp	caudal process	*lm*	lamina medialis
ct	cornu trabeculae	*pa*	processus antorbitalis
en	external naris	*pb*	planum basale
fen eth	fenestra ethmoidalis	*pnp*	prenasal process
fen ic	fenestra infra-conchalis	*pt*	planum tectale
fne	foramen nasalis externus	*pv*	planum verticale
fni	foramen nasalis internus		



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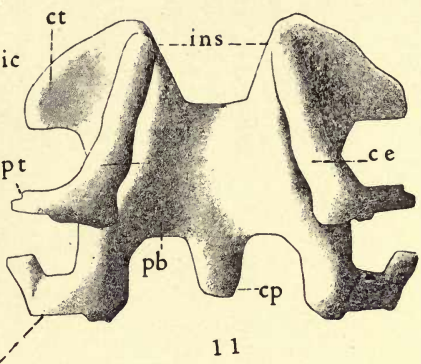

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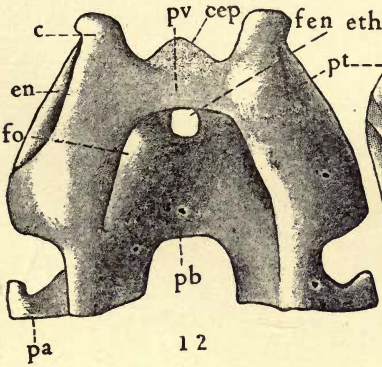

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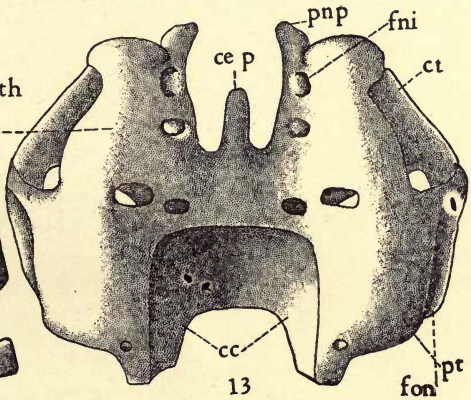

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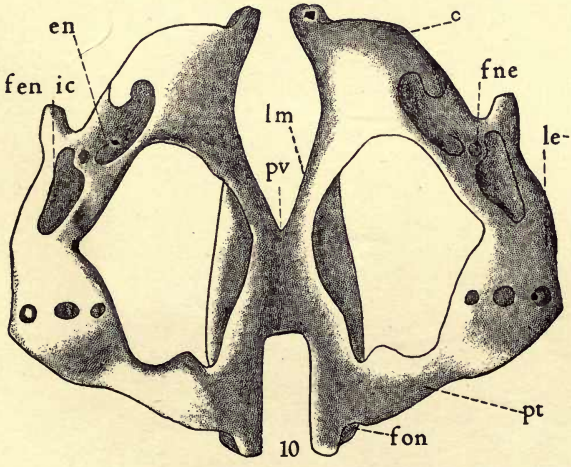

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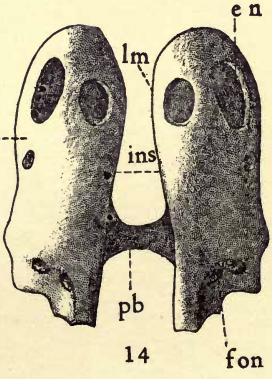

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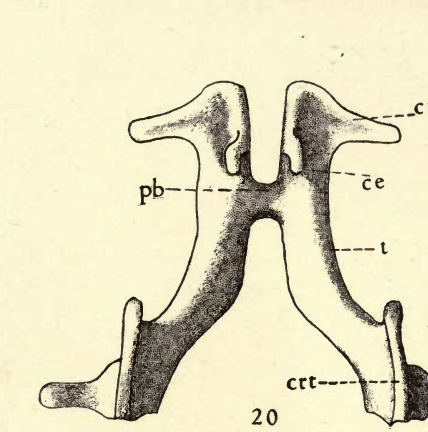
PLATE III

EXPLANATION OF PLATE

Fig. 15.—Dorsal view of model of nasal capsule of an adult *Diemictylus viridescens*.
Fig. 16.—Dorsal view of model of nasal capsule of *Triton cristatus* 28 mm. long.
Fig. 17.—Dorsal view of model of nasal capsule of *Triton cristatus* 35 mm. long.
Fig. 18.—Dorsal view of model of nasal capsule of *Spelerpes bilineatus* 15 mm. long.
Fig. 19.—Dorsal view of model of nasal capsule of *Spelerpes bilineatus* 37 mm. long.
Fig. 20.—Dorsal view of model of nasal capsule of *Spelerpes bilineatus* 46 mm. long.

c	cupola	*ins*	internasal space
ee	columna ethmoidalis	*lm*	lamina medialis
cr t	crista trabeculae	*pa*	processus antorbitalis
ct	cornu trabeculae	*pb*	planum basale
cn	external naris	*pe*	pons ethmoidalis
fen eth	fenestra ethmoidalis	*pnp*	prenasal process
fen ic	fenestra infra-conchalis	*pt*	planum tectale
fo	foramen olfactorius	*t*	trabecula
fon	foramen orbito-nasalis		



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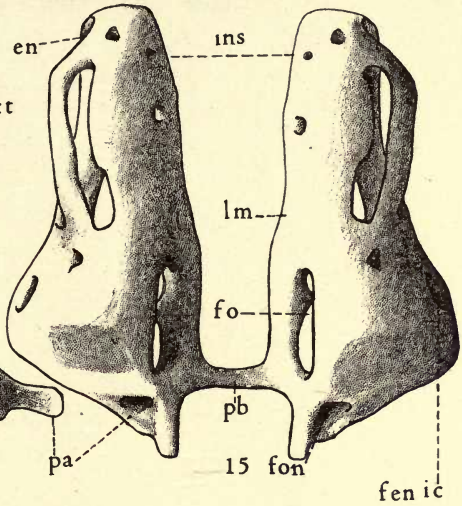

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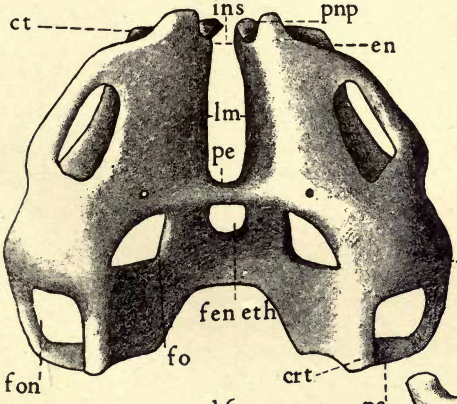

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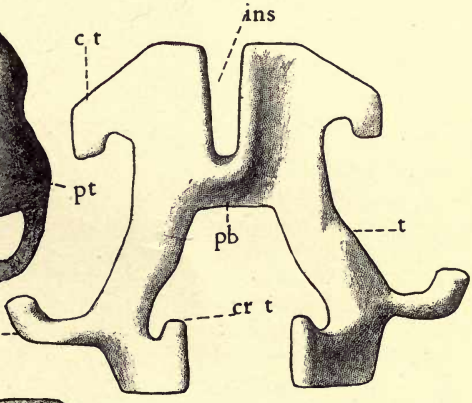

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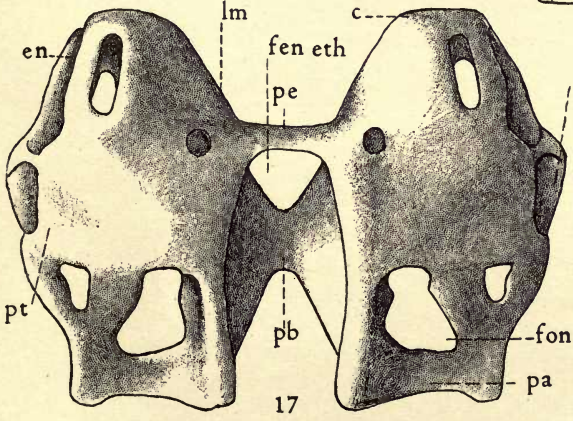

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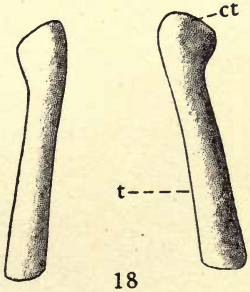

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PLATE IV

EXPLANATION OF PLATE

Fig. 21.—Side view of model of nasal capsule of *Spelerpes bilineatus* 46 mm. long.
Fig. 22.—Side view of model of nasal capsule of *Cryptobranchus alleghaniensis* two weeks old.
Fig. 23.—Dorsal view of model of nasal capsule of *Cryptobranchus alleghaniensis* five weeks old.
Fig. 24.—Ventral view of model of nasal capsule of *Cryptobranchus alleghaniensis* three months old.
Fig. 25.—Dorsal view of model of nasal capsule of *Necturus maculatus* 25 mm. long.
Fig. 26.—Dorsal view of model of nasal capsule of *Necturus maculatus* 30 mm. long.
Fig. 27.—Dorsal view of model of nasal capsule of a young adult of *Plethodon erythronotus*.

c	cupola	*mni*	median nasal incisure
ce	columna ethmoidalis	*pa*	processus antorbitalis
cr t	crista trabeculae	*pb*	planum basale
ct	cornu trabeculae	*pnp*	prenasal process
en	external naris	*pp*	pterygoid process
fne	foramen nasalis externus	*pt*	planum tectale
ins	internasal space	*pv*	planum verticale
le	lamina externa	*q*	quadrate
lm	lamina medialis	*t*	trabecula

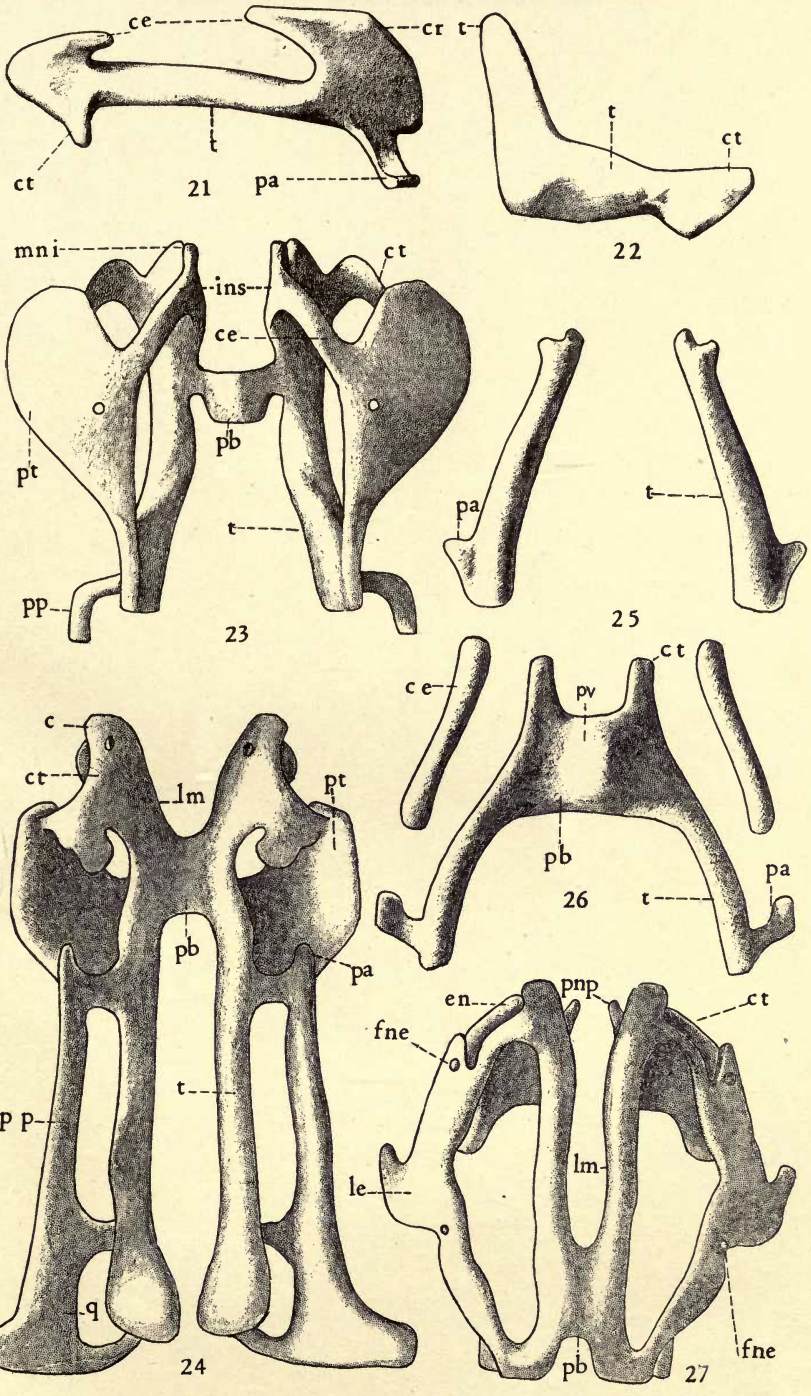
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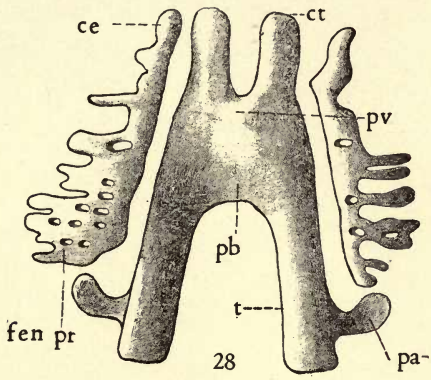
PLATE V

EXPLANATION OF PLATE

Fig. 28.—Dorsal view of model of nasal capsule of *Necturus maculatus* 45 mm. long.
Fig. 29.—Dorsal view of model of nasal capsule of a young larva of *Amphiuma means*.
Fig. 30.—Ventral view of model of nasal capsule of an older larva of *Amphiuma means*.
Fig. 31.—Dorsal view of model of nasal capsule of *Amphiuma means* 82 mm. long.
Fig. 32.—Dorsal view of model of nasal capsule of a young larva of *Epicrium glutinosum*.
Fig. 33.—Dorsal view of model of nasal capsule of *Epicrium glutinosum* 90 mm. long.

al p	alary process	*fne*	foramen nasalis externus
c	cupola	*fon*	foramen orbito-nasalis
ce	columna ethmoidalis	*ins*	internasal space
ce p	cephalic process	*le*	lamina externa
ch	choana	*pa*	processus antorbitalis
cr	circumnarial ring	*pb*	planum basale
cr t	crista trabeculae	*pob*	preorbital band
ct	cornu trabeculae	*pp*	pterygoid process
en	external naris	*pv*	planum verticale
fen pr	fenestrated process	*t*	trabecula



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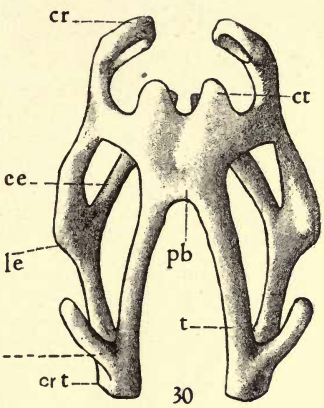

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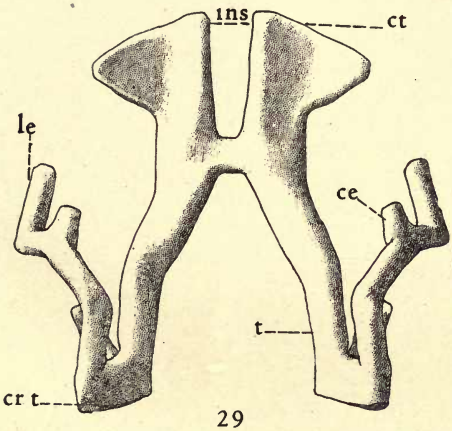

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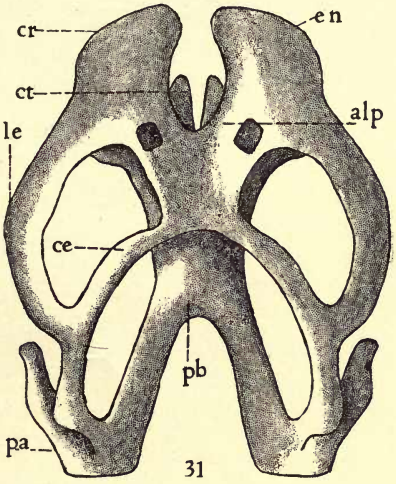

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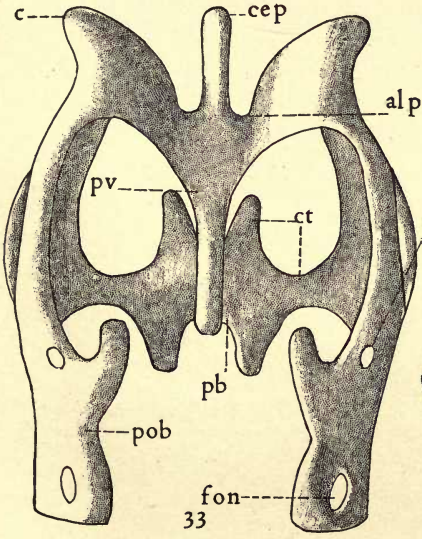

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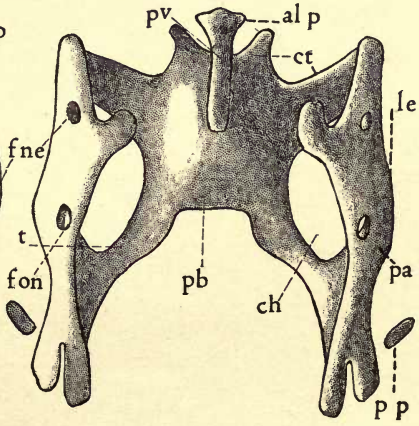

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PLATE VI

EXPLANATION OF PLATE

Fig. 34.—Dorsal view of model of nasal capsule of a young larva of *Pipa americana.*

Fig. 35.—Ventral view of the same model of *Pipa americana.*

Fig. 36.—Dorsal view of model of nasal capsule of *Bufo americana* 9 mm. body length.

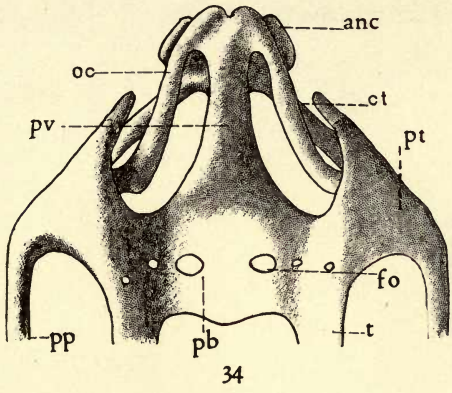
Fig. 37.—Posterior view of anterior half of model of nasal capsule of *Bufo americana* 9 mm. body length.

Fig. 38.—Dorsal view of model of nasal capsule of the adult *Hyla pickeringii.*

Fig. 39.—Side view of model of nasal capsule of the adult *Hyla pickeringii.*

Fig. 40.—Dorsal view of model of nasal capsule of *Rana viridescens* 28 mm. total length.

anc	alinasal cartilage	*la*	labial cartilage
ce	columna ethmoidalis	*le*	lamina externa
ci	cavum inferius	*mpq*	muscularis process of quadrate
cm	cavum medium	*oc*	oblique cartilage
cs	cavum superius	*pe*	pons ethmoidalis
ct	cornu trabeculae	*pb*	planum basale
en	external naris	*pp*	pterygoid process
fen nb	fenestra naso-basalis	*pt*	planum tectale
fni	foramen nasalis internus	*pv*	planum verticale
fo	foramen olfactorius	*qe*	quadrato-ethmoidalis process
fon	foramen orbito-nasalis	*sa*	solum anterius
ins	internasal space	*spc*	superior prenasal cartilage
ipc	inferior prenasal cartilage	*t*	trabecula



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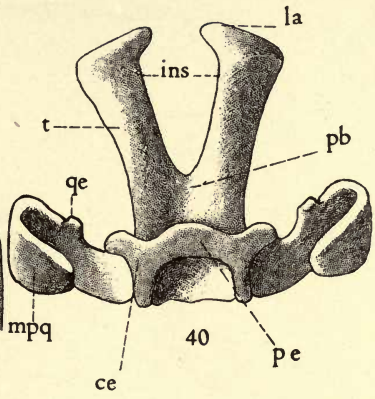

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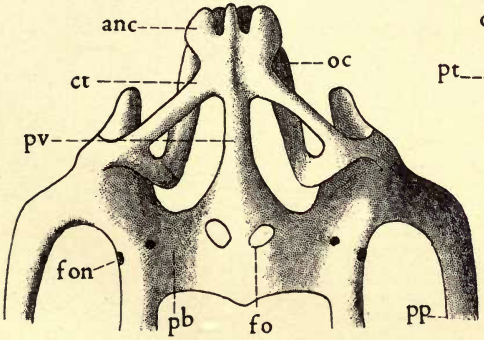

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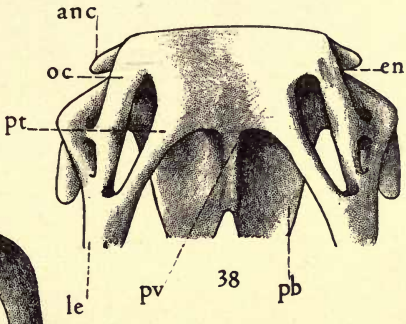

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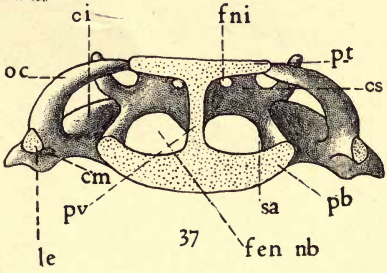

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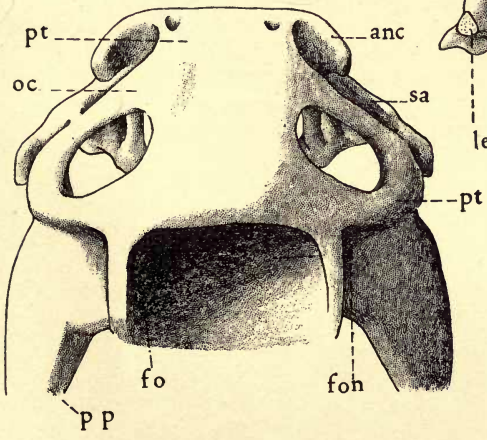

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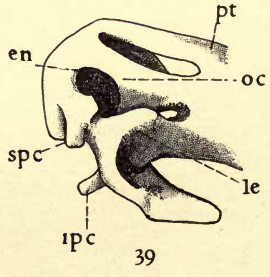

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PLATE VII

EXPLANATION OF PLATE

Fig. 41.—Transverse section through the anterior part of the nasal organ of *Amblystoma punctatum* 13 mm. long.

Fig. 42.—Transverse section through the middle region of the nasal organ of the same animal.

Fig. 43.—Transverse section through the choanal region of *Amblystoma punctatum* 20 mm. long.

Fig. 44.—Transverse section through the pons ethmoidalis of *Amblystoma punctatum* 25 mm. long.

Fig. 45.—Transverse section just anterior to the planum verticale of *Amblystoma punctatum* 55 mm. long.

Fig. 46.—Transverse section through the planum verticale of same animal.

Fig. 47.—Transverse section through the planum verticale of *Amblystoma punctatum* at the end of metamorphosis.

Fig. 48.—Transverse section through the lamina medialis of same animal.

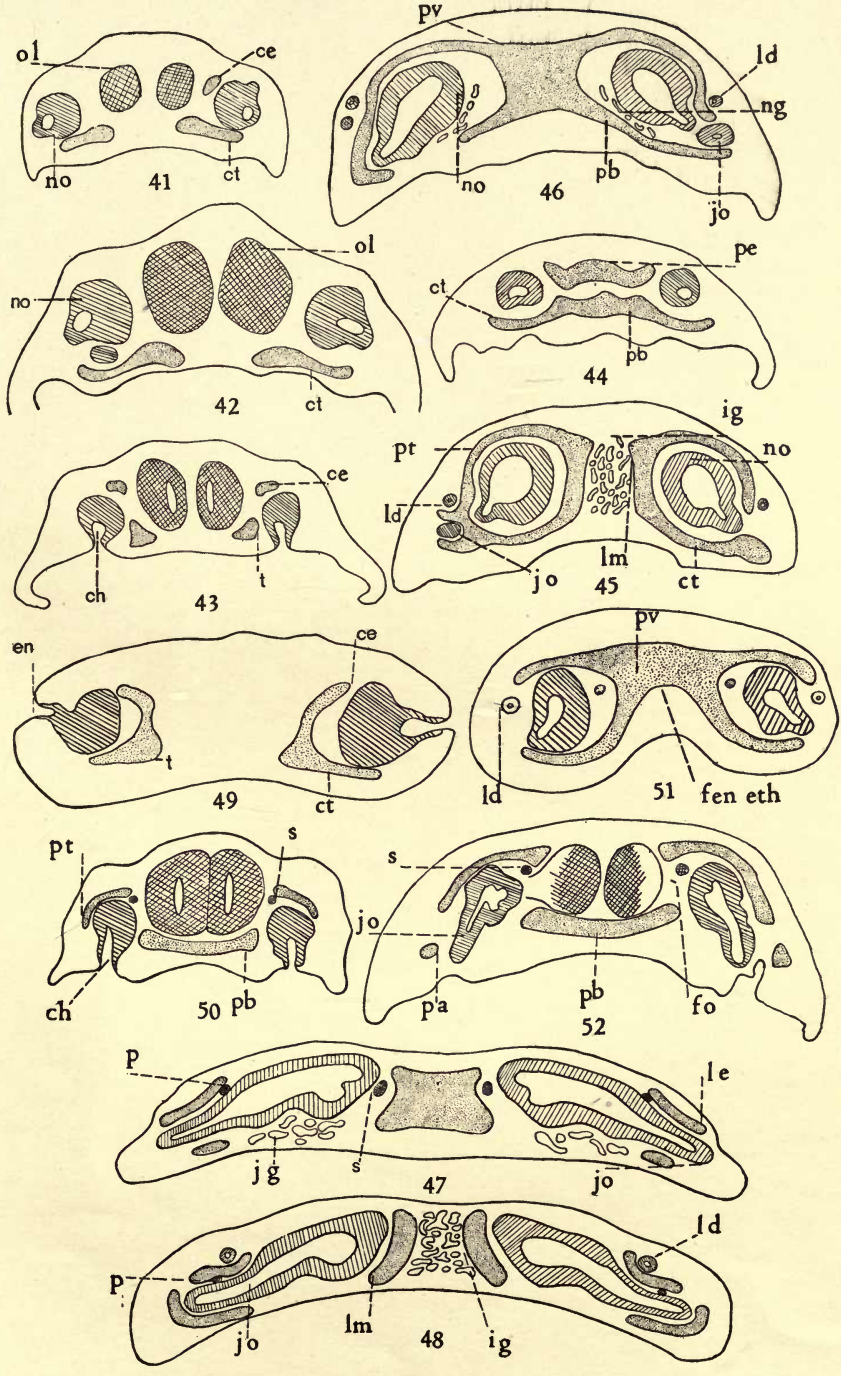
Fig. 49.—Transverse section through the external naris of *Salamandra maculata* 25 mm. long.

Fig. 50.—Transverse section through the choana of the same animal.

Fig. 51.—Transverse section through the fenestra ethmoidalis of *Salamandra maculata* 38 mm. long.

Fig. 52.—Transverse section through the planum basale of *Salamandra maculata* at the end of metamorphosis.

ce	columna ethmoidalis	*ng*	nasal glands
ch	choana	*no*	nasal organ
ct	cornu trabeculae	*ol*	olfactory lobe
en	external naris	*p*	profundus branch of the fifth nerve
fen eth	fenestra ethmoidalis	*pa*	processus antorbitalis
fo	foramen olfactorius	*pb*	planum basale
ig	intermaxillary gland	*pe*	pons ethmoidalis
jg	glands of Jacobson	*pt*	planum tectale
jo	organ of Jacobson	*pv*	planum verticale
ld	lacrimal duct	*s*	superficialis of the fifth nerve
lm	lamina medialis	*t*	trabecula
le	lamina externa		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en
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t
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ld
51
fen eth
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s
ch
50 pb
s
jo
p'a
pb
fo
52
P
le
jg
s
47
jo
ld
P
lm
jo
48
ig

PLATE VIII

EXPLANATION OF PLATE

Fig. 53.—Transverse section through the foramen olfactorius of *Diemictylus viridescens* 38 mm. long.

Fig. 54.—Transverse section through the anterior part of the nasal organ of the same animal.

Fig. 55.—Transverse section through the foramen olfactorius of the adult *Diemictylus viridescens.*

Fig. 56.—Transverse section through the pons ethmoidalis of *Triton cristatus* 28 mm. long.

Fig. 57.—Transverse section through the planum basale of *Triton cristatus* 35 mm. long.

Fig. 58.—Transverse section through the planum basale of *Cryptobranchus alleghaniensis* five weeks old.

Fig. 59.—Transverse section through the anterior end of the nasal organs of *Spelerpes bilineatus* 15 mm. long.

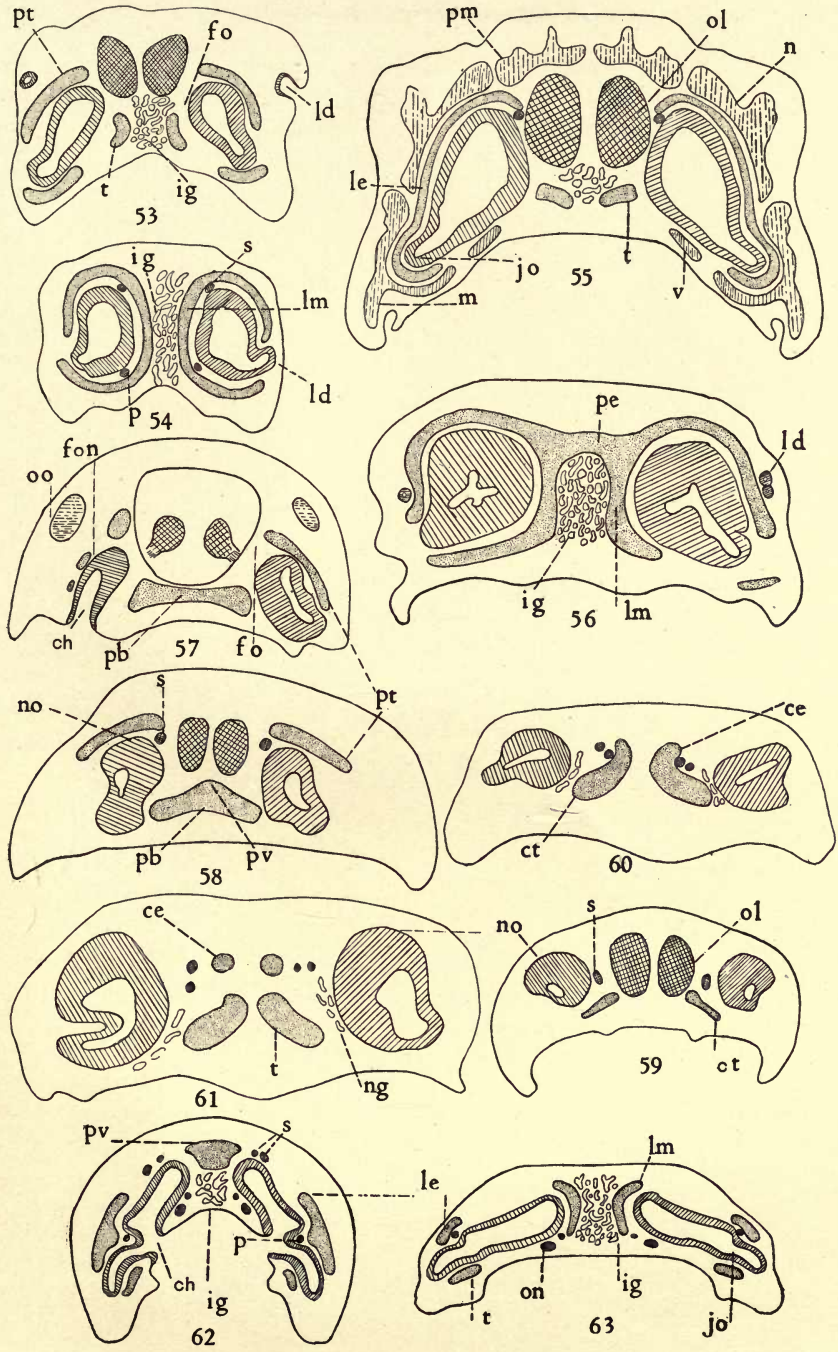
Fig. 60.—Transverse section just anterior to the planum basale of *Spelerpes bilineatus* 37 mm. long.

Fig. 61.—Transverse section through the same region of *Spelerpes bilineatus* 46 mm. long.

Fig. 62.—Transverse section through the choanal region of *Plethodon erythronotus* adult.

Fig. 63.—Transverse section through the lamina medialis of the same animal.

ce columna ethmoidalis
ch choana
ct cornu trabeculae
fo foramen olfactorius
fon foramen orbito-nasalis
ig intermaxillary gland
jo organ of Jacobson
ld lacrimal duct
le lamina externa
lm lamina medialis
m maxillary bone
n nasal bone
ng nasal glands
no nasal organ
ol olfactory lobe
on olfactory nerve
oo optic organ
p profundus of the fifth nerve
pb planum basale
pe pons ethmoidalis
pm premaxillary bone
pt planum tectale
pv planum verticale
s superficialis of the fifth nerve
t trabecula
v vomer



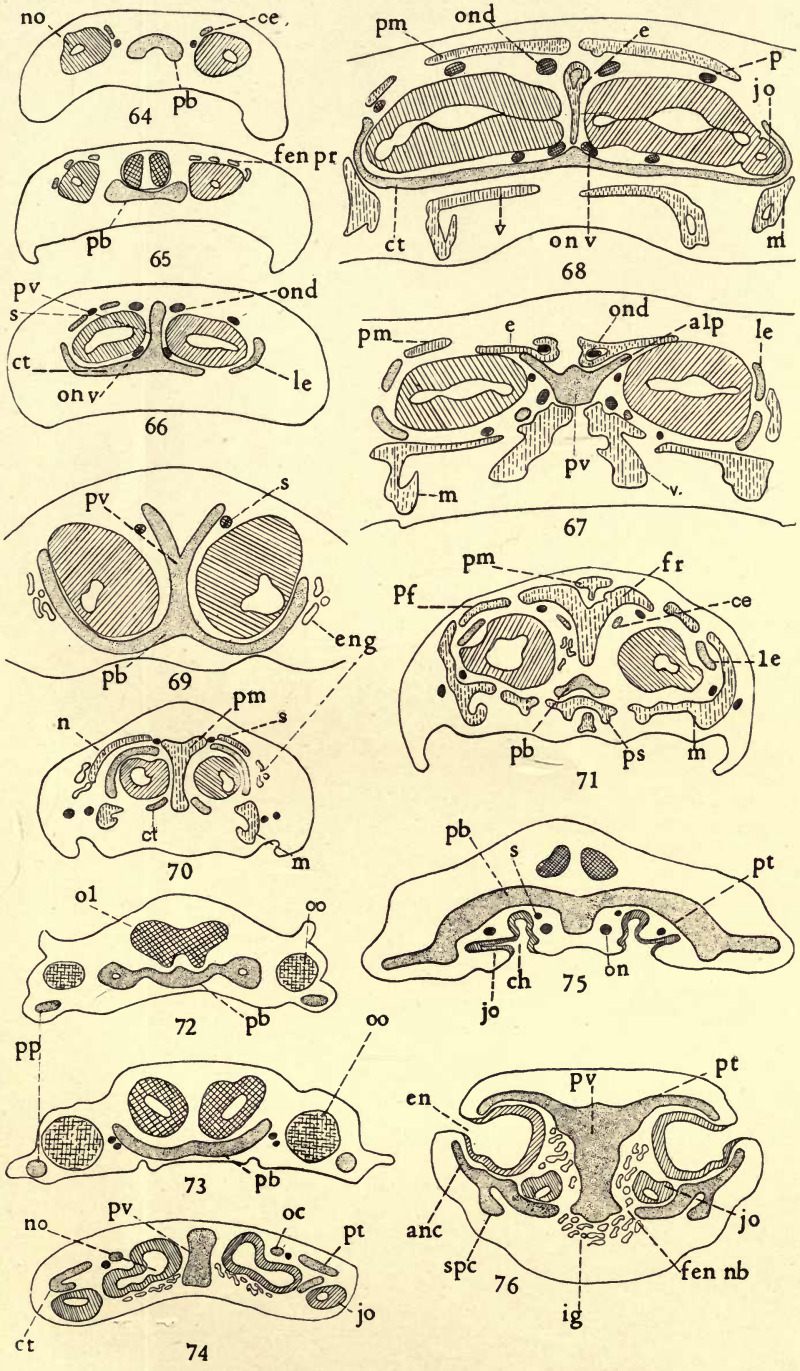
HIGGINS NASAL ORGAN IN AMPHIBIA PLATE VIII

PLATE IX

EXPLANATION OF PLATE

Fig. 64.—Transverse section through the planum basale of *Necturus maculatus* 30 mm. long.
Fig. 65.—Transverse section through the posterior part of the fenestrated process of *Necturus maculatus* 45 mm. long.
Fig. 66.—Transverse section through the planum verticale of the younger larva of *Epicrium glutinosum*.
Fig. 67.—Transverse section through the same region of a 90 mm. Epicrium.
Fig. 68.—Transverse section through the planum basale of the same animal.
Fig. 69.—Transverse section through the planum verticale of the older *Amphiuma means* larva
Fig. 70.—Transverse section anterior to the planum verticale of *Amphiuma means* 82 mm. long.
Fig. 71.—Transverse section through the planum basale of the same animal.
Fig. 72.—Transverse section through the anterior planum basale of a larva of *Pipa americana*.
Fig. 73.—Transverse section slightly posterior to the above.
Fig. 74.—Transverse section through planum verticale of *Pipa americana*.
Fig. 75.—Transverse section through the choanal region of *Pipa americana*.
Fig. 76.—Transverse section through the external naris of *Hyla pickeringii*.

al p	alary process
anc	alinasal cartilage
ce	columna ethmoidalis
ch	choana
ct	cornu trabeculae
e	ethmoid bone
en	external naris
eng	external nasal glands
fen nb	fenestra naso-basalis
fen pr	fenestrated process
fr	frontal
ig	intermaxillary gland
jo	organ of Jacobson
le	lamina externa
m	maxillary bone
n	nasal bone
no	nasal organ
oc	oblique cartilage
ol	olfactory lobe
on	olfactory nerve
ond	dorsal root of olfactory nerve
onv	ventral root of olfactory nerve
oo	optic organ
p	profundus branch of the fifth nerve
pb	planum basale
pf	prefrontal
pm	premaxillary
pp	pterygoid process
ps	parasphenoid
pt	planum tectale
pv	planum verticale
s	superficialis of the fifth nerve
spc	superior prenasal cartilage
v	vomer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anc
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76
fen nb
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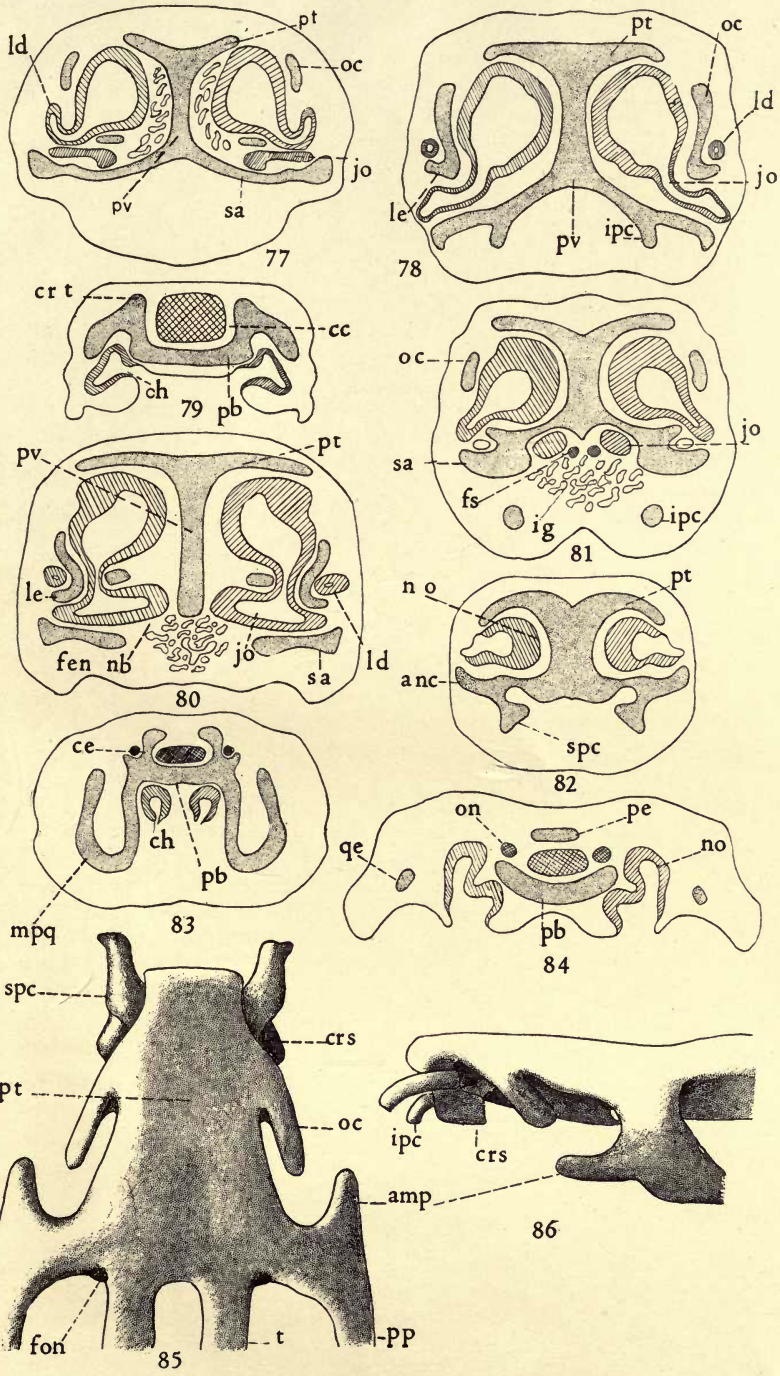
74

PLATE X

EXPLANATION OF PLATE

Fig. 77.—Transverse section posterior to the external naris of the adult *Hyla pickeringii.*
Fig. 78.—Transverse section through the lamina externa of the same animal.
Fig. 79.—Transverse section through the choana of a 9 mm. *Bufo americana.*
Fig. 80.—Transverse section through the fenestra naso-basalis of Bufo.
Fig. 81.—Transverse section slightly anterior to the preceding section.
Fig. 82.—Transverse section through the external naris of the same animal.
Fig. 83.—Transverse section through the muscularis process of the quadrate of *Rana viridescens* 28 mm. long.
Fig. 84.—Transverse section through the pons ethmoidalis of the same animal.
Fig. 85.—Dorsal view of model of the nasal capsule of a young adult of *Rana viridescens.*
Fig. 86.—Side view of model of the nasal capsule of the same animal.

amp	anterior maxillary process	*le*	lamina externa
anc	alinasal cartilage	*mpq*	muscularis process of quadrate
cc	cavum cranii	*no*	nasal organ
ce	columna ethmoidalis	*oc*	oblique cartilage
ch	choana	*on*	olfactory nerve
cr s	crista subnasalis	*pb*	planum basale
cr t	crista trabeculae	*pe*	pons ethmoidalis
fen nb	fenestra naso-basalis	*pp*	pterygoid process
fon	foramen orbito-nasalis	*pt*	platum tectale
fs	frontal branch of superficialis	*pv*	planum verticale
ig	intermaxillary gland	*qe*	quadrato-ethmoidalis
ipc	inferior prenasal cartilage	*sa*	solum anterius,
jo	organ of Jacobson	*spc*	superior prenasal cartilage
ld	lacrimal duct	*t*	trabecula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